Vol. 22 No. 4

April, 1956

THE BOTANICAL REVIEW

Interpreting Botanical Progress

Drought Resistance in Woody Plants.....JOHNSON PARKER 241

FUTURE CONTENTS
ON INSIDE BACK COVER

Published Monthly except August and September
Box 749, Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
HENRY ALLAN GLEASON and EDMUND H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
EDMUND H. FULLING

Advisory Editors

PROF. CHESTER A. ARNOLD
University of Michigan
PROF. MYRON P. BACKUS
University of Wisconsin
PROF. HERBERT C. HANSON
Catholic University of America
PROF. M. M. RHOADES
University of Illinois
PROF. GILBERT SMITH
Stanford University
DR. RUSSELL B. STEVENS
National Research Council
PROF. S. F. TRELEASE
Columbia University
PROF. CONWAY ZIRKLE
University of Pennsylvania

THE BOTANICAL REVIEW is published monthly except August and September. Subscription rate for all countries is $6.00; single copies: current volume, 75¢; previous volumes, $1. All subscriptions are payable in advance at par in Lancaster, Pa., or New York. Checks should be made payable to THE BOTANICAL REVIEW.

Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

Missing numbers can not be supplied without charge unless notice is received within two months after appearance of issues concerned.

All correspondence should be addressed to THE BOTANICAL REVIEW, at Box 749, Lancaster, Pa., or Fordham P. O., New York, N. Y.

THE BOTANICAL REVIEW

VOL. XXII APRIL, 1956 No. 4

DROUGHT RESISTANCE IN WOODY PLANTS

JOHNSON PARKER[1]

Department of Biological Sciences, University of Idaho, Moscow, Idaho

Introduction 241
Historical Background 244
Problems of Approach 251
Effects of Excision 251
Determining Viability 253
Difficulties in Comparing Arithmetical Values 255
Factors Contributing to Drought Resistance 257
Desiccation Resistance 257
Roots and Drought-Resistance Adaptations 262
Stems and Drought Resistance 266
Leaves and Drought Resistance 269
a. Overall leaf character 269
b. Stomate action 271
c. Leaf water content 274
d. Hairs and coatings 276
Bibliography 278

Introduction

It has been said that no other single factor determines the character of the earth's vegetation so much as does water (Walter, 1949: 109). Many of us who live in mountain country might not agree with this, but very often it is moisture and not so much temperature that determines the distribution of forest vegetation in such regions. In any case it is obvious that plants, since they emerged from their original water environment, have developed through the course of evolution an enormous variation in adaptations which appear to have survival value in coping with a varying water supply. Considering this great diversity of structural differences among plants, it should be no surprise that a subject like "drought resistance" cannot easily be interpreted in the course of a few experiments. Added to the genetic variations, there are often extensive changes

[1] We are indebted to Paul J. Kramer, Durham, North Carolina, and Arthur Pisek and Walter Larcher, Innsbruck, Austria, for their numerous helpful suggestions on certain sections of this paper.

induced by the kind of environment in which a plant is grown (Tumanov, 1927). Before indulging in further discussion, a few definitions should be made.

In science, definitions are frequently made but are seldom in complete agreement with one another. One of the most simple and yet complete definitions gave "drought resistance" as the capacity to survive periods of drought with little or no injury (Meyer and Anderson, 1952: 263); drought itself was defined as a period during which the soil contains little or no water which is available to plants, although these writers pointed out that drought is not subject to any rigid definitions. Nevertheless, rigid definitions have been attempted. The British meteorologists defined "absolute drought" as a period of 14 or more consecutive days without rain (Funk and Wagnalls, 1917), and the U. S. Weather Bureau defined drought as a period of 21 days or longer when the rainfall is but 30 per cent of the average for the time and place, but the considerations of Thornthwaite indicate that such definitions do not necessarily characterize soil moisture conditions (Encyc. Britt., 1954). Beard (1944) felt that evaporation should be considered as well as the soil water availability. This would seem to be an improvement on Kincer's concept (Daubenmire, 1947: 110) that drought is simply the number of consecutive days without significant precipitation. Daubenmire, however, went on to state that the evaporation factor should be included if data are available.

One sometimes finds the word "drouth" in the literature, but this appears to be only a synonym of "drought", and the latter is usually preferred. The origin of both words seems to be from the Old English "drūgath", thence to Middle English "droght" or "drougth" (Webster, 1955) and perhaps also to the obsolete word "droghte", and finally to "drouth" and "drought". These words correspond to the German "Dürre" or "Trockenheit" and French "sécheresse". Höfler and co-workers (1941) preferred the word "Dürreresistenz" for drought resistance and "Austrocknungsresistenz" for desiccation resistance, following the usage of Iljin (1930)[2]. This was later translated to English and used by

[2] However, the definition of "Austrocknungsresistenz" given by Migsch, cited in Höfler, Migsch and Rottenberg (1941), is slightly different from Iljin's.

Levitt (1951). We will also follow this procedure, namely, that "desiccation resistance" refers to the resistance of tissues to low water content without any particular adaptations for water content control, but that "drought resistance" is the overall resistance to drought. "Protoplasmic resistance" should probably be used only for resistance of the protoplasm itself.

The word "xerophyte" is, of course, of much more recent origin, evidently invented by Clements (1902) and used to refer to a plant that can resist drought. This idea was based on field observations and was, therefore, a phytogeographic instead of a physiological concept. In contrast to this, many of the early workers about the turn of this century, e.g., Jost, Schimper and Kamerling, performed some simple experiments and concluded that the definition of a "xerophyte" should be made on a physiological basis. Jost, for instance (cited by Kamerling, 1917), stated that plants of drier habitats which exhibit decreases in transpiration should be called "xerophytes". Schimper (1903: 2) also felt that it was one of the adaptations of xerophytes that they can reduce transpiration to low levels. Kamerling, however, on the basis of his own experiments felt that no very clear definitions could be made, since, for instance, many trees which survive seasonal drought in the tropics, during which time they shed their leaves, can lose enormous amounts of water during the wet season. In spite of this, he finally concluded that xerophytes are plants which require relatively little water for their normal life processes (Kamerling, 1917).

This concept was apparently exchanged during the 1920's for the more general usage, and Huber's definition has been widely accepted (Höfler, Migsch and Rottenburg, 1941), namely, that all plants which can withstand physiological drought of the soil or high evaporation of the air without suspension of their life processes are to be called "xerophytes". Maximov (1929b: 249) also took this general stand and concluded that xerophytes are simply plants that are exposed to a deficient water supply; on the other hand, in contrast to the early German workers, he considered "true xerophytes" to be plants that can withstand large water losses without dying.

At the recent International Botanical Congress, Stocker (1954) stated that Kamerling's question: "Which plants shall we call

xerophytes?" is obsolete, for the reason that a single group of plants, all growing in the same apparently droughty location, have so many overlapping and interblending adaptations that no clear lines among them can be drawn at all. In other words, the convenient and long-accepted classification of Shantz (1927) would seem to be rather artificial, since many of the "drought-enduring" species probably possess a number of adaptations besides mere desiccation resistance.

In this paper, therefore, we plan to consider the main points which might influence the total or overall drought resistance of a plant, namely, the "constitutional resistance" of Stocker (1951). This is not the same as Biebl's meaning applied to marine algae (Biebl, 1949, 1952). It is also of importance to consider the resistance of a species as a whole, including its life cycle, in contrast to the resistance of its photosynthetic organs alone (Walter, 1931: 111), and we intend to include these considerations in this discussion.

Historical Background

The oldest ideas concerning various disturbances to plants go nearly as far back as recorded history. As was the case with chemical theory, an understanding of water relations had to await the development of sound concepts of the physical state of matter. Evaporation and condensation were largely misunderstood through most of the Middle Ages, and the concept of "vapors" was so closely entwined with supernatural forces that it remains for most of us in our present materialistic age as only of historical interest (Pachter, 1951). One of the best reviews of the ancient ideas of disease arising from non-parasitic causes is contained in Sorauer (1933: 3).

With few exceptions, such as the work of Stephen Hales (1727) on water translocation in trees, the problem was not seriously approached until the middle of the last century. Robert Hartig (cited in Büsgen and Münch, 1929: 307) measured the water content of 30 species of trees at various times of the year and found definite fluctuations in this content which seemed related to environmental changes. The decrease in water content in late winter was believed to be caused in certain species of trees by decrease in absorption of water by roots in comparison to continued loss from the leaves (Kosaroff, 1902).

Although considerations of transpiration may seem to have little to do with the problem of drought resistance in the light of Maximov's publications (cited below), it is nevertheless well to consider some of the early work in this extensive field. Transpiration rates of young trees were measured by the phytometer technique in the previous century (von Höhnel, 1879), and the water transpired from different species was compared. Later critics pointed out that these figures were based on fresh weight and therefore had little meaning for entire trees, since some trees have far greater leaf mass than others. Huber (1953) has recently discussed this problem and summarized much of the information.

Furthermore, as Büsgen and Münch (1929: 304) pointed out, transpiration is influenced not only by the amount of leaf but also by the quality of site and by water availability at different times of year. These writers also reflected the widely-held concept that as water becomes limiting, the stomate action of the tree leaves tends to retard water loss and thus to make adjustments, an idea later expressed by Huber (1931). The fact that transpiration may diminish soon after the water content of the soil falls below the field capacity but before the ultimate wilting point is reached has been pointed out by a number of writers (Gradmann, 1932; Furr and Reeve, 1936; Schneider and Childers, 1941; Loustalot, 1945; Lane and McComb, 1948; and reviewed by Kramer, 1949: 63). On the other hand, Veihmeyer and certain others (cited by Kramer, 1949: 62) felt that water is equally available to the plant down to the wilting point.

In considering the succulents, the idea of plants maintaining their water content at high levels in time of drought is quite obvious. But this idea was extended to many other kinds of plants at an early time. Schimper (1903) was one of the first to notice that many arctic plants have succulent characteristics and suggested that this is an adaptation to "physiological drought" produced by the frozen condition of the soil. Also, in studying tropical vegetation he concluded that water retention plays an important role in survival of many of the species growing in regions of seasonal drought. Other writers of the early part of this century did much to forward the idea of water retention in many other kinds of plants. Kamerling (1917), for instance, in Rio de Janeiro found that excised leaves (severed at the petiole) of

Ficus elastica dried out in about six days in the shade, but excised leaves of *Philodendron pertusum* lasted in a fresh condition for 31 days in the shade. This was explained by the low transpiration rate from the leaves of the latter plant, amounting to only 0.7 per cent of its total leaf weight each day. Judging from Sachs's early experiments (cited in Bonner and Galston, 1952: 151), the loss of weight due to respiration would be a negligible percentage of the loss in weight attributable to water lost. We have calculated from the respiration (CO_2 released), of *Pinus ponderosa* leaves (Parker, 1954b) that only about four per cent of the weight loss in the first four days after excision is due to respiration at 25° C.

Although water retention seems to be a factor of importance in many plants, the idea has sometimes been carried to extremes. It was often felt that xerophytes are plants that transpire very little water (see introduction of this paper). In contrast to these ideas, Maximov (1923; 1929a), and closely followed by Alexandrov (1924), Mittmeyer (1931) and Haas and Halma (1932), found that certain xerophytes transpire fully as much as mesophytes when water is readily available. Furthermore, Maximov and Krasnosselsky-Maximov (1924) found that the level to which a plant can be dried without killing it varies widely from species to species. This idea had already been propounded for woody species in an unpublished doctoral dissertation some years before (Schröder, 1909) and has since been cited by Maximov (1929b: 243). The idea of high resistance of the cells of mosses to dehydration had been forwarded by Holle (1914), and the idea of a lethal level of moisture content had been presented by Neger and Fuchs (1915) for conifer leaves sometime before Maximov's publications on the subject. But Maximov realized the importance of the concept and went so far as to state that Schimper was in error (Maximov, 1929a). This point of view was soon given added strength by Iljin's oft-cited work (Iljin, 1930, 1932, 1933, 1935) and more recently by that of many others, for instance, Höfler, Migsch and Rottenburg (1941) and Höfler (1950). About the time that Maximov's early papers appeared, Korstian (1924) also suggested that the "density of the cell sap" (osmotic concentration of expressed cell contents determined cryoscopically) is associated with drought resistance in many conifers of the western United

States: the higher the density the more resistant they were supposed to be.

As a result of this work there has been a tendency, especially in this country, for physiologists to regard desiccation resistance as of prime importance in explaining drought resistance. At the same time the idea of lowered transpiration rate during a drought has seemed to have fallen into disfavor. This has been partly caused, perhaps, by a reaction against the teleological explanations so often found in the older texts, but also by the fact that water relations of plants have largely become the realm of ecologists, while many physiologists with their ever-growing interest in biochemistry have regarded many phases of water relations as pure ecology and of no interest to them.

Another of the older ideas that has now fallen largely into disrepute is that many semi-desert plants with supposedly higher osmotic concentrations and thus higher diffusion pressure deficits can withdraw more water from the soil than those with lower osmotic concentrations (Fitting, 1911). However, Curtis and Clark (1950: 160) have argued that these high osmotic concentrations are probably a result of the environmental conditions under which the plants are grown and not something characteristic of xerophytes. Marshall (1931), in reviewing the problem, cited several writers who believed that drought resistance might be estimated in terms of the amount of soil moisture remaining when wilting occurs. But as Curtis and Clark pointed out, in the range of the wilting percentage, only slight changes in the water content result in very great changes in the forces with which water is held in the soil, so that whether a plant has a higher diffusion pressure deficit than another or not would make little difference. The fact that various kinds of plants have essentially the same wilting point was made clear by Briggs and Shantz (1912), although Marshall (1931) gave Cameron and Galagher in 1908 credit for having been earlier in this discovery.

Another idea related to this was that high osmotic concentration can appreciably retard transpiration (Fitting, cited by Maximov, 1929b: 273), but this was disputed by both Livingston and Renner, according to Maximov. The table presented by Bonner and Galston (1952: 108) would suggest that with low vapor pressures in the air, these differences in osmotic concentration could not

account for much variation in water loss. However, under conditions of high atmospheric vapor pressure, the situation could be quite different. Furthermore, the experiments of Boon-Long (1941), carried out in Curtis's laboratory, indicated that considerations based on theoretical values, such as those of Bonner and Galston, may be sound in themselves but do not apply where membranes and cell walls are concerned. One rather convincing experiment showed that, when a collodion membrane was placed over a 1 M sugar solution in water, evaporation from the collodion, which was quite permeable to water, was decreased to one tenth of the evaporation from the solution without the collodion. Boon-Long explained this on the probability that the solute concentration was higher in the capillaries of the membrane because of evaporation. Other experiments of his would seem to indicate that increasing the sugar content of leaf cells does, indeed, greatly decrease transpiration without any change in stomate opening. Perhaps one could criticize his method of determining stomate opening, but other experiments seem well founded. In this connection it is of interest to note that Stålfelt (1932) and Pisek and Berger (1938) found that as the leaf dehydrates, cuticular transpiration decreases (see also Shreve, 1931).

Still another idea involving osmotic concentration was that it influences the desiccation resistance, perhaps through its effect on the protoplasm and vacuole. Although variations in osmotic concentration have been shown to have little or no absolute association with either cold or desiccation resistance, an annual increase in osmotic concentration seems to reflect chemical or physical changes that, to use Levitt's expression, constitute a sort of second line of defense to damage from cold (Levitt, 1941) and thus perhaps also to desiccation, although Höfler, Migsch and Rottenburg (1941) felt that osmotic concentration itself can not be used as a criterion of drought resistance, since some drought-resistant plants have a low osmotic concentration and some non-resistant ones have a high osmotic concentration. Diurnal as well as seasonal fluctuations in this value were studied in *Metasequoia glyptostroboides*, and a considerable part of the osmotic concentration was believed to be caused by the presence of K^+ and Cl^- as well as sugars (Kurimoto, Takada and Nagai, 1954).

In considering the plant as a whole, however, a number of other

adaptations have to be included. Huber (1924, 1935) and also Thoday (1931) concluded that effectiveness of absorbing surface, resistance of conductive system, and area of transpiring surface all play a role in the water economy of a tree. This will be considered in the sections on root, stem and leaf adaptations in this paper.

Also in recent years we have seen the acceptance of the basis of the water-maintenance concept together with that of the desiccation resistance concept. For instance, Pisek and Berger (1938) made it clear that there are distinct differences in water retentive capacity of various coniferous leaves when they are excised and that, although this constitutes their main source of resistance to drought, there are also slight differences in desiccation resistance among different species. Chu (1936) also found differences in lethal level of moisture content in leaves of various woody plants, but distinct differences between certain of the species are not very clear if one examines his data. Schopmeyer (1939), on the other hand, felt that water retention in leaves of *Pinus echinata* plays a role in drought resistance of this species.

It seems fairly obvious that, even though some plants may lose large quantities of water when the soil has ample moisture, they may be able to decrease this transpiration to low levels during time of drought, an idea stated by Weaver and Clements (1938: 445) and more recently by Walter (1949: 248). Actually even Maximov (1929a) made some remarks to this effect in spite of his criticism of Schimper. In fact Maximov quoted Bergen and also Guttenberg to point out that water loss can be reduced to very low levels in some plants (Maximov, 1929b: 266) and that this can influence drought resistance (Maximov, 1923, 1929b: 390).

Höfler and his associates (1941), who did much to forward the idea of desiccation resistance, stated that drought resistance is the sum of all factors which enable the plant to persist on a dry habitat and to survive a drought period: transpiration regulation, water storage in tissues, development of high osmotic pressure . . . , better water conduction, as influenced by root system and capacity of the conductive system . . . , and finally the ability to withstand water-lack through severe wilting without damage.

Experiments of Parker (1951, 1952a, 1954c) with Rocky Mountain conifers seem to agree in their results with those of Pisek

and Berger (1938), although we noted no particular differences in desiccation resistance among different species. It was concluded that many adaptations play a role, including water content of the trunk, branches and twigs, so that no one factor can be said to be the only one in making one species of conifer more drought resistant than another. Even though plasmolysis experiments indicate some slight differences among species in resistance to this treatment, results of slow cooling and thawing (1° C./hr. change) showed no appreciable differences between *Abies grandis* and *Pinus ponderosa*, although their resistance fluctuated greatly with the season (Parker, 1955a). This fact suggests little difference in desiccation resistance in these species, although *Pinus ponderosa* is considerably more drought resistant than *Abies grandis*, at least when about three years old.

It is one of the interesting recent developments that an increase in resistance to cold has been closely related to an increase in resistance to desiccation (Siminovitch and Briggs, 1953; Pisek and Larcher, 1954). This idea is actually not new, since Maximov (1914) and Harvey (1918) proposed it many years ago, but it is much better established today. Furthermore, these hardiness changes can be related to changes in resistance to plasmolysis and deplasmolysis in solutions (Siminovitch and Briggs, 1953).

We are then led to inquire as to the causes of this resistance, and although many have considered the protoplasm to be of prime importance, Höfler (1950) and Levitt (1951) have pointed out that desiccation resistance and cold resistance affect more than just the protoplasm. Höfler (1950) stated that death results from desiccation, as we have known since Iljin, more because of mechanical causes which are dependent on the construction of the cell wall, the thickness of the wall coatings and the size of the vacuole, than upon the inner characteristics of the plasma as such. The protoplasmic field itself is very complicated, and the literature deals not only with zoological and botanical treatments but also with those of physical chemistry (e.g., Jones and Gortner, 1932).

In such a complex field it is to be expected that there would be some sharp disagreements over the state of the protoplasm in the "hardened" and "unhardened" condition. Some workers have believed that the protoplasm becomes more viscous on hardening to cold (Kessler and Ruhland, 1938); others have thought

it becomes less viscous (Scarth and Levitt, 1937). Some have thought that the protoplasmic structure tends to open up on hardening to cold, but that it becomes more firmly bound on hardening to desiccation (Stocker, 1951), an idea which seems to have its origin in the work of Schmidt (1939). Stocker's concept has been considered by Levitt (1951) to be based on non-existent evidence. Changes in permeability have also been associated with hardening, but permeability to one compound seems to increase while permeability to another decreases (see below under desiccation resistance).

The problems to be solved would seem to lie largely in the changes of the cell contents with hardening, including the vacuole as well as the cytoplasm. Considering the water economy of the whole plant, much has yet to be learned about vital resistance (Stocker, 1954), i.e., when the plant is not killed by a drought but comes under a certain amount of stress, and this might be of importance to future growth and competition with other species. For instance, more needs to be known of the changes in photosynthesis with dehydration of the tissues, although this has already been studied to some extent (Iljin, 1923; Heinicke and Childers, 1936; Stocker, 1937; Kozlowski, 1949; Bormann, 1953; Eckhardt, 1953; Negisi and Sattoo, 1954, 1955b).

Problems of Approach

EFFECTS OF EXCISION

In order to determine whether a certain adaptation is of any survival value to the plant in times of low soil or atmospheric moisture, the investigator is, of course, confronted with conducting an experiment that is free of influences besides those he wants measured. Perhaps the simplest type of experiment is the one involving the whole plant, as, for instance, with the phytometer technique. But the fact that one species lives longer than another in un-watered phytometers, as in the experiments of Daubenmire (1943) with Rocky Mountain conifers or of Parker (1952b) with southeastern conifers, may be revealing for their absolute drought resistance but does little to indicate what might happen in less severe droughts and also little to explain what causes this resistance.

Ordinarily we are forced to dismember the plant in some way

to test one organ at a time, and this leads at once to other influences. Excision of the branch or twig may, in some cases, lead to fundamental changes which make the experiment of no value. For instance, a cut twig of *Pinus austriaca*, even though cut under water and kept with the cut end submerged, may not take up enough water to compensate for foliar losses. This may be caused by blocking of the functioning xylem with resinous exudations, although we have not proven this. A twig of *Thuja plicata*, on the other hand, usually continues in a viable condition for many weeks when cut under water and left with its cut end in a jar of tap water.

Dismemberment of the leaves is even more dangerous, since the food exchanges to the stems are cut off. The effect of shock does not appear to be of any significance in excision of conifer leaves, but the mere act of cutting is believed sometimes to cause stomate closure in some plants (Curtis and Clark, 1950: 223, citing Knight, 1917). The only original paper we have found on this is that of Laidlaw and Knight (1916) which showed that about seven minutes after severing there was a slight opening of the stomates in leaves of various species. Electrical relationships also may be varied by cutting as in oat coleoptiles which are mechanically stimulated (Schrank, 1944) or in coleoptiles which are killed in certain areas by boiling (Lund, 1947: 54).

Judging from the results of tissue culture work, excision itself is not a matter causing great difficulty. In our work with conifer leaves it appeared that they could be excised and kept alive in the dark for several weeks if kept hydrated and free of attacking organisms. Viability was indicated by the leaf's normal dark green color, its flexibleness, the normal appearance of the cell contents, and a positive tetrazolium test. Clark (1954) showed that excision of conifer leaves did not affect the photosynthetic rate for several minutes after severing and Negisi and Sattoo (1955a) found no appreciable change in photosynthesis of a severed shoot until one or two hours after excision. Shoots which were not placed with their severed ends under water declined in photosynthesis more rapidly than those which were.

The biochemical changes in an excised leaf would appear to be of more serious nature than the immediate effects of cutting. Bonner (1950: 299), citing various writers, discussed the changes

that occurred in excised leaves of certain herbaceous plants. In general, protein seemed to be hydrolyzed and asparagine accumulated in the leaf after severing. During the first two days, respiration (CO_2 release) may show a decline. Bonner discussed how excised leaves of barley in the dark showed a decline in CO_2 released, and this appeared to be associated partly with a decrease in sucrose content and perhaps also in starch and certain other carbohydrates. In excised conifer leaves we also noticed a rapid primary decline in CO_2 released after excision (Parker, 1952a), but other effects were also involved, such as the warming and handling of the leaves. The respiration, however, then steadied off and remained so for several days in spite of slow dehydration.

DETERMINING VIABILITY

COLOR CHANGES. Many workers have simply used color variations as criteria of changes from living condition to death. In some species this seems sound enough, as, for instance, in some of the broad-leaved species which show a browning and drying up of leaves. But whether the leaf turns brown or not depends on light intensity during dehydration (Parker, 1953b) as well as on temperature. Larcher (1954) used the transparency of leaves to light as a criterion of loss of life. In algae, Ogata and Nagai (1954) extracted the pigments and measured their absorption in a spectrophotometer. They found a decline in most all wave lengths in absorption after the cells had been damaged in certain ways. Dryness or crispness of a leaf might seem to be a good criterion of death, yet Iljin (1933) was of the opinion that if rehydrated slowly enough, the tissue might often be revived.

GAS EXCHANGE. Measurements of carbon dioxide released from the organism in question are open to a certain amount of question, not only because of the fact that the release of CO_2 is not an exact measure of the chemical changes in the cells but also because it does not give an accurate measurement of the energy being released in respiration (Curtis and Clark, 1950: 516). Under carefully controlled conditions and realizing its shortcomings, it seems to be a useful tool in studying drought resistance (Montfort and Hahn, 1950; Stocker, 1951), especially where a constant recording apparatus, such as the infra-red gas analyzer with a point recorder, can be used (Huber, 1950; Parker, 1953a). The intro-

duction of the Beckman oxygen analyzer should also be useful in measuring instantaneously the amount of O_2 in an air stream.

ELECTRICAL MEASUREMENTS. In recent years studies of electrical relations in living tissues, perhaps beginning with the work of Osterhout (1922) and later by Luyet (1932), Rosene (1935), Schrank (1944) and Lund (1947), have shown that it is possible to measure electrical fields and currents in living cells. One of the advantages of the method of Greenham and co-workers (1950, 1952) for determining viability in plants was believed to be that the use of simple wire probes left the tissue intact for other measurements. Greenham and associates (1952) made their measurements of conductivity at audiofrequency and used an A.C. bridge of the variable resistance type; potential differences across the probe points were determined by a vacuum tube voltmeter. Changes in capacitance as well as equivalent parallel resistance were associated with the dying of the plant tissue. Although water content of the tissue affected results, the method seemed promising to these investigators. In connection with this, the potentials of tumerous tissue from tomato plants were found to be different from those in tissue of normal tomato plants (Wilcox, Knight, and Bless, 1953).

ENZYME MEASUREMENTS. In seed analysis, enzyme tests, such as the test for catalase, have long been experimented with, but none has been so useful and trouble-free as tetrazolium salts, in particular, light-sensitive 2,3,5-triphenyltetrazolium chloride (TTC) (Kuhn and Jerchel, 1941). The original warning of these writers that it might indicate but not necessarily prove viability has been borne out by subsequent work. There has been some research, however, which appears to discredit the method as a proof of viability (Gunz, 1949; Brown, 1954).

The reliability of TTC as a viability indicator has been discussed by Parker (1953a, 1953b, and 1955b). It was concluded that although reduction of TTC and its closely allied derivatives might not always be a good indication of viability since they can be reduced by various non-living means, their lack of reduction in cells which normally reduce them is a fairly sure sign of the lack of viability.

Reduction of TTC is carried out normally through the action of

succinic and isocitric dehydrogenases in corn embryos as well as by certain oxidases and possibly other related enzymes; also these reactions may be mediated by diaphorase (Throneberry and Smith, 1953). Blue tetrazolium, a ditetrazolium salt, may be reduced by a somewhat different group of dehydrogenases and oxidases (Dianzani, 1953). It is of interest that blue tetrazolium is not only light-stable, and thus unlike TTC, but also fluorescent in ultraviolet light.

DYES AND FLUORESCENCE. The method often used in determining viability of cells has been the dye penetration test, either into or out of the cells (for example, Siminovitch and Briggs, 1953; Etz, 1939; both of whom used neutral red). Ordinarily tissue slices are used, soaked in a solution of the dye, and the presence of the dye determined under the microscope.

Another variation on microscopic techniques has been the use of fluorescence. One method is to employ a dye that is fluorescent in ultraviolet light and to determine its penetrability into the cell (Strugger, cited in Parker, 1952a, 1953b). Among the various fluorescent substances, rhodamine B has recently been used with good success (Keller and Chiego, 1949). Changes in the intensity of the natural or "primary" fluorescence of the cells has been mentioned by Parker (1952a, 1953b) and by Larcher (1953). Biological applications of fluorescence microscopy have been reviewed by Ellinger (1937) and Richards in Mellors (1955: 5/22). Luyet and Gehenio (1936) and Brumberg and Larinow (1947) showed that some kinds of cells change in their absorption of ultraviolet light as they die.

DIFFICULTIES IN COMPARING ARITHMETICAL VALUES

Plant physiologists have long been plagued by difficulty in arithmetically expressing their data in comparing one species with another. A good example of this is in the comparison of percentage values of water content between two species. If both plants were constructed alike, the difficulty might be resolved, but they never are exactly alike.

Suppose, for example, we have a leaf with a great deal of water-containing xylem and another with very little such xylem. The latter probably would have more living cells than the former. If both tissues were dehydrated to the same extent, both losing the

same amount of water, the former would probably show a movement of water from the xylem tissue into the living cells, while the latter would show little such movement. Although both leaves might lose the same amount of water, the former would have living cells which might well have more water than the latter leaf. Such a shift of water during dehydration is not mere theory, since Ursprung and Blum (1945) demonstrated its occurrence in dehydrating conifer leaves.

One way of avoiding some of this difficulty in comparing the water content of one species to that of another is to use the saturation weight of the leaf and to involve other factors so as to come out with something which might appear, at least, to be better. Stocker (1929a) used the saturation water content (the most water the leaf cells can hold) in estimating daily variations in water content in one plant, a situation which seems mathematically sound enough in itself. Stefanoff (1931) also made use of the concept, but Höfler, Migsch and Rottenburg (1941; also reviewed in Levitt, 1951) went much further than this. They used it to compare lethal levels of water content in different plants. However, if we substitute algebraic symbols for their expressions, the meaning of the formula can be better realized:

Let x = the saturation weight of the leaf
a = the fresh weight
b = the dry weight
c = the weight of leaf at lethal level of water content.

Then according to their system we have:

$$(100) \cdot \frac{x-a}{x-b} = \text{natural saturation deficit} \qquad (1)$$

and

$$(100) \cdot \frac{x-c}{x-b} = \text{critical saturation deficit} \qquad (2)$$

The authors then divide expression (1) by (2) and we get

$$\frac{(100)\ (x-a)}{x-b} \cdot \frac{x-b}{(x-c)\ (100)} = \text{“ plant requirement ”}$$

It will be seen that the $x-b$ factors and 100's cancel out and that we end up with $(x-a)/(x-c)$. Aside from the introduction of the saturation weight we still have the fresh weight factor and we still have the lethal level of water content, each affected by

anatomical variations among species. Regardless of how ingenious the formulae become, it appears that in the end they do not escape from the fundamental difficulty. Runyon (1936) concluded that we have no method for determining water content, even in the protoplasm, and he quoted Vassiljev (1931) who found that saturation water content determinations could easily be too high. Nevertheless we entirely agree with Höfler et al. that the use of the saturation water content would appear to be of special importance in calculating water deficits in leaves of such species as *Larrea tridentata,* since under drought conditions the "normal" leaf water content may be far below it. Pisek and Winkler (1953) compared in tabular form the amount of dry weight and water content above and below the lethal level as a percentage of the saturation weight in several plants. The variations from plant to plant were quite marked, although a number of species had certain values roughly in common so that they could be grouped together. In conclusion, it appears that there is no way of expressing lethal levels by a percentage value so that one species can be compared in its desiccation resistance with absolute infallibility with another, but that, if we confine ourselves to species of rather similar structure, the errors should be at a minimum.

Factors Contributing to Drought Resistance

DESICCATION RESISTANCE

It is difficult to distinguish between the resistance of an entire cell and that of its protoplasm alone (Höfler, 1950; Levitt, 1951). It would thus appear that the atmospheric desiccation method so commonly used to test tissues, measures the entire cell, and perhaps tissue resistance, instead of the resistance of the protoplasm alone. The size of a cell has been suggested to be of importance (Iljin, 1935; Siminovitch and Briggs, 1953). Also its shape and the size of the vacuole as well as the vacuolar composition have been considered to be of importance in withstanding desiccation (Iljin, 1935). Höfler (1950) also mentioned cell wall structure in this connection. We are therefore confronted with numerous factors which enter into a study of desiccation resistance.

Changes that occur in the protoplasm have received a large amount of attention, and a sort of unified picture has been presented by Stocker (1951) which sums up much of his previous

work and that of many others. Some of this is unfortunately in unpublished doctoral dissertations and thus hard to judge; in fact his conclusions have been sharply criticized by Levitt (1951).

Stocker pictured the protoplasm as a lattice-work of thread-like protein particles filled with water, in which salts, sugars and proteins are dissolved or suspended. The condition of this lattice-work is pictured as controlled by "Haftpunkte" or points of adhesion, by which the protein molecules are connected. These points of adhesion may be chemical valence bonds, electrical attractive forces or adsorptive forces. The hardening of an intact plant, which was brought about by depriving the soil of added water for a period of time, was believed to result in a firmer binding of these protein threads, and this, in turn, was supposed to be associated with an increase in structural viscosity and a decrease in pore-permeability (to water and urea). In cold resistance, on the other hand, Stocker pictured an opening of the lattice system, resulting in increased pore-permeability and stronger hydration. That drought hardening and cold hardening might be two different processes was also suggested by results of his school which showed an increase in respiration after exposure of plants to drought but a decrease in respiration after subjection to cold with subsequent warming. A great deal of his theory seems to be based on the results of shaking experiments of Kahl (1951; also discussed by Stocker, 1948) and on a comparison of such changes as those of respiration after shaking to those after subjection of a plant to drought. Simonis (1952) also explained this respiratory change on the basis of changes in the protoplasmic structure and in spatial relationships within the protein network.

In any case these theories seem hard to reconcile to the idea that cold resistance (involving slow cooling and warming: 1° C./hr. change) and desiccation resistance undergo a nearly simultaneous change in a great many plants (Siminovitch and Briggs, 1953; Pisek and Larcher, 1954). In answering the question that this problem poses, Stocker (1955) considers that the effects of drought on the protoplasm take place in two stages: the reaction phase and the restitution phase, the first involving disorganization, loosening of the fibrils, and decrease in viscosity, the second involving hardening, reorganization, and increase in viscosity. Since some investigators have measured one phase and others another, results are difficult to compare.

The conditions of protoplasm are extremely complicated, if we are to judge from the works of such investigators as Frey Wyssling (1953) and DeRobertis, Nowinski and Saez (1954). Apparently we are dealing with an enormously variable structure, even in one kind of cell, to say nothing of the variation between species. Ultra-centrifugation and the electron microscope in particular have revealed that there are in general four fractions containing enzymes: (a) nuclei, (b) mitochondria (visible under the ordinary microscope), (c) microsomes (submicroscopic), and (d) ground plasma (DeRobertis et al., 1954: 359). The mitochondria themselves are quite complex and apparently have their own membranes. The spatial arrangement of enzymes on or in the mitochondria is not known. Also the general mass of the cytoplasm is different in its outer portion, as can be shown by centrifuging intact cells. Evidently it has a sol-gel interchangeability that is more or less unique in certain kinds of cells. That these membranes are not simply interphasic states of the cytoplasm and that they may play an important role in prevention of rupture of the cytoplasm during shrinking with dehydration or with plasmolysis has already been considered (Scarth, Levitt, and Siminovitch, reviewed in Curtis and Clark, 1950: 289). According to their theory, the ectoplasm becomes more fluid in cold-hardened cells. It is possible that changes in permeability would also be accounted for by changes in this outer layer of cytoplasm. On the other hand, according to Priestley (1930) the cambial cells of certain trees pass entirely into a gel state at the start of the dormant season and return to a sol state in spring. Bailey (1954: 39) described some marked changes in vacuolation in conifer cambial cells with the season that might be related to Priestley's observations.

Respiration rate changes should also be carefully considered. A great many different things can cause these changes. We have found, for instance, that the speed of drying makes a difference in the respiratory rate as measured by CO_2 release (Parker, 1952a), although perhaps here we are dealing with a climacteric such as that found in ripening fruits (Biale, 1950) and not with changes in intact plants with hardening. The respiration rate also may go into a climb after desiccation treatment with subsequent rehydration (Montfort and Hahn, 1950); the greater the climb, the greater the damage to the protoplasm is assumed to be. Negisi

and Sattoo (1955b) found that excessive as well as deficient watering of intact woody plants causes subnormal respiration rates.

Short term changes in CO_2 release rates are often of a different nature, being caused by such things as alteration of quantity of substrate. This change is quite remarkable in such material as tissue slices in a Warburg manometer when the tissue is starved and then has glucose added. Other changes may also be involved. Millerd, Bonner and Biale (1953) have investigated the causes of the respiratory rise in ripening avocado fruits and concluded that in unripened fruit the respiration is limited by the capacity of the phosphorylation system. They found that the rate of substrate oxidation by respiratory particles was dependent upon the concentration of phosphate acceptor. Although the rate of substrate oxidation is normally limited by this capacity to the phosphate accepting system, the limitation can be removed with such a substance as 2,4-dinitrophenol which severs the coupling of mitochondrial oxidation to oxidative phosphorylation. The climacteric rise (increase in O_2 uptake) was then concluded to be caused probably by an uncoupling process.

Perhaps these changes are not related in any way with those of hardening or of protoplasmic disarrangement, and probably O_2 intake and CO_2 release do not necessarily represent respiration to the same degree, but in any case it can be seen that respiratory rises and decreases can be caused by numerous factors.

Still other considerations should enter into a study of hardening. It would seem that we are dealing not only with biochemical changes during hardening but also with grosser changes which are indicated by such conditions as the clumping of the chloroplasts, appearance of thread-like strands (visible in photomicrographs of Kessler and Ruhland, 1938), changes in vacuolation, and differences in the shape of the plasmolyzing cell contents. Borriss (1938), however, has pointed out that the appearance of plasmolysis (convex or concave) is different in different plants and can be varied by using different plasmolyzing media, a point which may be a criticism of Kessler and Ruhland's work.

At present the problem of structural viscosity of protoplasm would seem to be one of the centers of attention in explaining hardiness, and yet there have been some fundamental disagreements on this. Thus Kessler (1935) forwarded the idea that when a plant becomes frost-hardy, its protoplasmic viscosity in-

creases and it is therefore more difficult to rupture and kill by dehydration accompanying slow freezing. Scarth and Levitt (1937), on the other hand, felt that the viscosity decreases on hardening, thus making the protoplasm more fluid and less likely to rupture. In a later paper Kessler and Ruhland (1938) considered Scarth and Levitt's paper in some detail and produced further evidence to support their own conclusion. The lowered rate of chloroplast sedimentation in intact cells was believed by Kessler and Ruhland to indicate an increase in viscosity. Schmidt, Diwald and Stocker (1941) came to the conclusion that the viscosity of the plasma is a structural viscosity dependent on two components: the viscosity or flowability of the inner solution (Zwischenflussigkeit) and the frictional resistance of the lattice framework. Levitt (1951) later concluded that increase in frost hardiness is associated with a looser binding of the fibrils and did not mention viscosity, a value which seems hard to measure. This, in turn, was believed to be related to a higher degree of hydration of proteins. Perhaps also there is an increase in total water-soluble protein, a fact demonstrated to be related, although not precisely so, to an increase in hardiness to cold in *Robinia* bark (Siminovitch and Briggs, 1948; Briggs and Siminovitch, 1948).

The idea of "bound water" has prevailed for some time (Meyer, 1932), although Weismann (1938) thought that it was a doubtful concept. So much seems to depend on the method of measurement that results are difficult to interpret (Levitt, 1951). Use of cells with large amounts of protoplasm instead of those with large vacuoles for experimentation would seem to be a matter of considerable importance in studying protoplasm effects (Levitt, 1951). The amount of total cell water was shown by Pisek and Schiessl (1939) with conifer leaves to play a role in cold resistance. Perhaps an increase in cell water entails an increase of "free" water over bound water. Whether such changes occur in the vacuole as distinct from the protoplasm is evidently not known, the two usually being studied together. Writers use the word "cell sap" quite freely, although their experiments do not mention any attempts to separate vacuolar from protoplasmic material.

Another change in protoplasm with hardening seems to be the greater permeability to water and certain organics (Scarth and Levitt, 1937), but this field has proven complicated. Apparently while there is an increase in glycerol permeability with hardening,

there is a decrease in urea permeability; in fact, plants have been classified according to their permeability to these two compounds after hardening. Also pH may affect these permeability results (Bogen, 1938; Drawert, 1948, 1954). Auxins seem also to affect permeability of both gelatins and protoplasm (Meinl and Gutenberg, 1952).

Apart from the purely physical changes there is considerable evidence that the increase in a number of compounds is associated to some extent with an increase in hardiness to cold (Levitt, 1941) and perhaps also to desiccation. In general, an increase in sucrose, glucose or water-soluble protein and a decrease in starch or certain minerals have each been found to be associated with but not entirely related to cold hardiness increases in different plants. For instance, in conifer leaves an increase in sugars seems to occur (Levitt, 1941, citing others), but in the bark of *Robinia pseudoacacia* an increase in water-soluble protein and a decrease in starch were best related to hardiness increases (Siminovitch and Briggs 1953; Siminovitch, Wilson and Briggs, 1953). Sugars were not regarded as primary factors in the frost hardiness mechanism of *Robinia* (Siminovitch and Briggs, 1948). Levitt (1954) suggested that an increase in cold hardiness might be related to an increase in a sugar-protein complex, not to the free sugars themselves, in some cases.

Other plants have been considered, such as *Larrea tridentata*, wherein the protein content was higher, the resins and nordihydroguaiaretic acid lower, in the more desiccation-resistant leaves (Duisberg, 1952). Other compounds that might be studied with profit are sometimes difficult to separate from interfering substances, such as glycerol, although paper chromatography offers a solution to the problem. This compound is known to produce artificially an increase in resistance to ice formation (Luyet and Gehenio, 1952), although this may be a different situation from desiccation accompanying extracellular freezing.

ROOTS AND DROUGHT-RESISTANCE ADAPTATIONS

In some geographical regions the roots of woody shrubs often reach into layers which remain above the ultimate wilting point for much, if not all, of the season, while the surface soil may dry out to very low moisture levels (Weaver and Clements, 1938: 320).

It would therefore be expected that depth of root would be of great importance to survival. Walter (1939) concluded that differences in root system often determine the survival of woody plants in the semi-desert regions of Africa, and Billings (1938) drew similar conclusions for some plants of North Carolina. The importance of deep roots is well exemplified by certain of the semi-desert shrubs of western North America, e.g., *Artemisia tridentata,* which seem to be indicators of plentiful sub-soil moisture, not of dry soil conditions (Hall and Clements, 1939). Reestablishment, however, is another problem, and only in exceptional years of good surface soil conditions can abundant seed grow into a few successful individuals (Daubenmire, 1947: 121; Walter, 1949: 110; Parker, 1954a). In forests the importance of early penetration of the root from tree seeds has been frequently pointed out (Haig, 1936; Toumey and Korstian, 1937: 141, quoting Holch, 1931, and Toumey, 1929; Coile, 1940; Kramer, 1949: 131; Sattoo and Namura, 1953). Other variations in roots are considered by Toumey and Korstian (1937: 137).

The total amount of absorbing surface, sometimes greatly influenced by the fact that some roots are continually growing into new areas in the soil (Kramer and Coile, 1940), may play an important role in survival. In fact, many years ago Pringsheim (1906) pointed out the importance of total root extent for the plant's water economy in several crop plants. In woody plants when the root-leaf ratio is high, the leaves have a higher transpiration rate per unit leaf surface than when it is low, other conditions being optimum (Bialoglowski, 1936; Parker, 1949). This suggests that when there are fewer leaves per amount of root, these few leaves are better hydrated. Variation in the ratio of root mass to top mass in different woody plants was thoroughly discussed by Huber (1924), and the amount of root was suggested by Lachenmeier (1932) to be of importance when the plant began to dehydrate to a slight extent and the leaves then tended to rely on root-absorption.

When, however, the entire soil mass dries down to levels near the ultimate wilting point, the root seems to become dormant or at least to cease growth. In this case, on a theoretical basis, the soil may continue to dehydrate, due to losses of water vapor from the soil surface to the air, and thus become reduced to levels approach-

ing the hygroscopic coefficient. Under these circumstances the relative humidity of the soil pore spaces might be so much reduced as to cause a measurable loss of water from the roots by transpiration, and in fact the root water could be replaced by water from the leaves. We have been able to demonstrate that uprooted pine seedlings translocate water downwards as the roots lose water (unpublished data), and Stone, Went and Young (1950) showed that leaves could absorb water vapor from the air under dry soil conditions with high atmospheric humidities. Stone and Shachorf (1954) showed that water can be transpired from roots while the leaves are sprayed with water. Under wilting conditions the growing root tips of *Pinus taeda* have been observed in glass boxes to shrink slightly and then apparently to die. At least the new growth, when the soil was again watered, was not from the growing tips but from points further back (unpublished data).

It would be expected that many of the outer cells in a greatly dehydrated root would die, assuming that they can not recover from air-dryness. This, however, is an assumption and is by no means well-established; little is known about drought resistance of roots as such. Water might be retained farther back in some kinds of roots at levels which might allow survival. Haberlandt (1928: 353) discussed experiments which indicated that water was retained within the endodermis of some kinds of plants under drought conditions. Dyes were found to enter the "penetration cells" of the endodermis but not the thick-walled endodermis cells themselves. Nevertheless, it is difficult to see how the endodermis is effective in retaining water unless it also excludes it to a large extent, a situation which would lead to low rates of water absorption. Possibly the penetration cells shrink with dehydration, while the thick-walled ones do not. Perhaps also these cells are extremely desiccation-resistant and do not rely on water retention for survival. On the other hand, extreme desiccation is probably unusual, since when the leaves of oaks have died from drought, the roots of the same seedlings may still have white viable tips (Bordeau, 1954). We have found that root-tips of *Pinus ponderosa* are killed by exposure to relative humidities of less than 95 per cent for four days.

If maize roots are grown in a soil that is frequently allowed to dry out to the wilting point, suberization seems to develop well

in the epidermal layers (Werner, 1931). According to Kramer (1949: 113), both the hypodermis and endodermis may become suberized in the older tissues during the first year. Only a few days of subjection to dry soil conditions may result in decreased root permeability in certain herbaceous plants (Kramer, 1950). He attributed decreased absorption to cessation of root elongation and increased suberization for the most part, although he felt that some decrease in protoplasmic permeability might also occur. In woody roots considerable water can evidently be absorbed through the bark, especially through the lenticels, breaks around branch roots, and wounds in the bark (Kramer, 1949: 116), although Huber in his 1952 lectures at the University of Munich mentioned that the last two means of entry are unlikely because of the chance of entry of pathogens. In any case it would be suspected that water could evaporate from roots under very dry soil conditions, probably through these same channels or directly through the phloem and periderm of the root bark.

The fact that soils may dry out to very low levels seems to be made clear by such workers as Boyko and Abraham (1954) who used the term "internal dew" to describe the phenomenon of condensation of water vapor in very dry soils. Such water was believed to be available to annuals like *Amaranthus blitoides* and to contribute to its survival in Palestine soils.

It may be argued that only seedlings are subjected to such severe dryness of the soil and that mature trees are seldom, if ever, subjected to complete drought, since their roots often penetrate deeply. We suspect, however, that trees which are weakened from the effects of drought are more readily attacked by various organisms, and thus the cause is attributed to some organism rather than to climatic conditions. Nevertheless there is ample evidence of fairly old trees suffering from drought. Boyce (1938: 52) cited, among others, Dunning (1925), Balch (1927), Coover (1930), Frothingham (1931), Perry and Knull (1931) and Boyce (1933), and discussed the work of Stickel (1933) and McIntyre and Schnur (1936). Other reports on drought damage to trees can be found in the work of Stiles (1935), Albertson (1940), Albertson and Weaver (1945), Lutz (1952) and Copeland (1955). Some kinds of leaf-fall have been also attributed to drought both in broad-leaved trees and in conifers (Sorauer, 1933: 429). Pool (1913)

also discussed leaf-fall from summer drought. Hartley and Merrill (1915) described marginal die-back of the leaves of *Acer platanoides* as well as yellowing of *Quercus palustris* leaves after a drought. Considering some effects on *Pinus contorta* in Colorado, Hartley and Merrill mentioned the discoloration of bark, usually to brown. They also mentioned that "white pine blight" (on *Pinus strobus*) was probably due to recurrent drought. Meinicke (1925), a pathologist, also pointed out that conifers and oaks in the Sierra Nevada often died in groups after severe soil drought, the injury showing in the tops and progressing downwards. During a drought the shallowest-rooted trees often were the ones to show the most damage (Meinicke, 1925; Shirley, 1934; Albertson and Weaver, 1945).

STEMS AND DROUGHT RESISTANCE

The adaptations of stems to drought are, of course, difficult to evaluate but can be divided into (*a*) water storage adaptations, (*b*) adaptations concerned with resistance to the movement of water, and (*c*) adaptations for the prevention of water loss from the stems.

Fluctuations in water content in trees have been known since the days of R. Hartig (cited in Büsgen and Münch, 1929: 307) and more recently have been considered by Langener (1932) and Huber (1952), and briefly reviewed by Parker (1954c). There seems to be little doubt that some of the trunk storage water is available to the leaves in time of low water absorption by the roots. Some of the water decline may be produced in the trunks by direct transpiration to the air, but this would seem to be relatively small. McIntosh (1949) considered that some trees could be "leaf seasoned" by leaving the branches and leaves attached after the trees were felled, but Smith and Goebel (1952) found little difference between trunk water content of felled trees of various species of the genus *Carya* with branches intact and with branches cut off. In citrus trees the water content of the fruits may also show a diurnal cycle of expansion and contraction (Bartholomew, 1926), somewhat similar to that demonstrated by MacDougal (1936) in tree trunks. The lemon fruits themselves were found to lose very little water by transpiration. These experiments indicate the importance of the interdependence of water contents in various parts of the tree.

As water is withdrawn from the wood, gases sometimes replace it. In some cases, however, a considerable vacuum may be produced which is evident when the trunk is penetrated with an increment borer and air can be heard entering the wound. On the other hand, there have been cases recorded in which the water came under great tension and, instead of pulling away from the cell walls, caused an internal rupture in the wood. This collapse or cracking of wood was observed by Day (1950, cited by Lutz, 1952) in living conifers in Great Britain and was associated with a severe drought in August. Lutz (1952) observed diamond-shaped openings in the wood of *Picea glauca* in Alaska and concluded that they must have been caused by tensions produced by condition of low water availability to the roots when transpiration continued from the leaves during the colder season. This is evidently quite different from "drought rings" which look like "frost rings" (discussed in Boyce, 1938: 50). The collapsed tissues described by Lutz resemble very closely those noted in kiln-dried timbers copiously illustrated by Tiemann (1941). One interesting thing about Lutz's paper is that it describes results which Greenidge (1954) would seem to predict in certain kinds of woods if tensions were to reach high values.

A consideration of resistance to water translocation in woody stems has been made by Huber (1928), and it appears that ring-porous woods, such as those of *Robinia pseudoacacia, Quercus pedunculata* and *Fraxinus excelsior*, which have very long uninterrupted channels through a series of vessel segments, sometimes the full length of the tree, are the least resistant to water translocation. Diffuse-porous woods, such as those of *Tilia tomentosa* and *Populus balsamifera*, which may have unbroken elements for only one or two meters, proved to be more resistant to translocation. Finally the conifers, which have no vessels at all, showed the greatest resistance to translocation. Speed of translocation in the intact tree using a thermocouple method was found to follow in the same order, the rates in the diffuse-porous woods being slower than those in the ring-porous woods. The rates were so slow in the conifers that the method was not applicable for accurate measurements (Huber, 1935; Huber and Schmidt, 1936; Huber, 1937). On the other hand, the drought-resistant shrub, *Larrea tridentata*, was found by Ashby (1932) to have nearly twice the resistance to water translocation as the mesophytic privet, a species of *Ligustrum*, of

similar size. But even in the leaves large resistance to flow is believed to be encountered across the protoplasts to the mesophyll (Shields, 1950, citing other writers). It would appear that each part of the plant contributes its own resistance to translocation, although some may produce very little, and that in a relatively large tree the trunk and branch friction may be considerable, but that ordinarily in small plants at least, the roots offer the greatest resistance to water movement from the soil on its path to the leaves (Kramer, 1938; Sattoo, 1949). Apparently this root resistance varies widely, depending on various treatments, such as drastic heating (Kramer, 1949: 202), amount of wilting (Kramer, 1950), flooding in closed containers (Parker, 1950), and the environment under which the roots are grown (Stocker, 1923).

Dehydration of stems of shrubs and trees, caused by direct water loss to the air, has been considered by Weaver and Mogenson (1919), Gordiagin (1930), Kozlowski (1943) and Geurten (1950). If one removes the leaves from practically any woody plant, transpiration from the remaining stem is very small, as would be expected, since there would be very large surface reduction. Actually the stems of such seedlings as those of oak in winter transpire about the same on a unit area basis as intact seedlings of various evergreen conifers, according to the statistically analyzed data of Kozlowski (1943). This seems to agree generally with results of Weaver and Mogenson (1919). It would be expected, however, that in certain other seasons, conifers might transpire considerably more than defoliated broad-leaved seedlings, especially on a seedling basis. Also there seems to be a species difference in amounts of water loss from excised defoliated branches of different conifers, although only a few individuals were tested (Parker, 1954c). In trees with lenticels more water seems to be lost through the lenticels than through the periderm (Wiesner and Pacher, 1875; Geurten, 1950).

An interesting feature of the stems of *Artemisia tridentata* which are subjected to rather severe atmospheric drought is the appearance of rings of corky tissue (interxylary cork) between the annual growth rings (illustrated by Diettert, 1937: 70, 73). He also pointed out that this condition occurred in certain other plants, and Diettert felt that these layers, some of which are suberized, might benefit the plant in semi-arid regions. How much water can be

absorbed into the stems from the bark has not been studied to any great extent, but MacDougal (1912) cited Lloyd who found that loose bark of *Fouquieria* could absorb water readily. This water was available to the cells inside the bark and could influence budding of the branch.

LEAVES AND DROUGHT RESISTANCE

a. OVERALL LEAF CHARACTER. Since Shields (1950, 1951) has already considered this subject in considerable detail, we will not consume so much space as a full treatment would deserve. It would, nevertheless, be of interest to supplement her reviews in certain ways.

One of the recent reviews of this subject is that of Walter (1949: 237). Like Shields (1950), he called attention to the frequent misinterpretation of so-called xeromorphic structures and pointed out that many of them may have little to do with the water economy of the plant. Quoting Zalenski and Kostytschev-Went, Walter stated that plants grown under bright light and under conditions enhancing rapid transpiration developed the following characters:

a) Greater thickness of leaf vein per leaf surface.
b) Greater number of stomate openings per surface.
c) Smaller size of stomates.
d) Smaller size of epidermal and mesophyll cells.
e) Greater number of hairs per surface, but less size of hairs.
f) Thicker outer walls of epidermis and cuticle.

Some of these same general considerations can be found in Maximov (1929b: 400) and in Höfler (1950). But here again it is uncertain whether the water economy of the plant is greatly improved by some of these changes. Maximov (1929b: 400) felt that in general these are adaptations of secondary importance in drought resistance, but this seems to depend on the species, even among common mesophytes (Pisek and Berger, 1938). Kramer (1949: 287) felt that it is probable that not all xeromorphic leaves are the result of water deficits, but that nutrition could play an important role.

Increase in volume of leaf venation may result in greater water availability because of lowered friction, but this might lead to a more rapid instead of a retarded transpiration. During periods

of high moisture stress, however, when the stomates might largely close, the situation could be quite different and the lag in water intake to the leaves might be partly benefited (overcome) by a lowered xylary friction, although this is probably a teleological point of view.

The greater number of stomates might seem to lead to higher transpiration than lower, although their diffusion shells may become more overlapping and thus interfere with one another. From a teleological point of view it might be thought that it would be of advantage to have more stomates on leaves of "xerophytic" plants in certain spacial arrangements because if water conditions were favorable better gas exchange could occur during the little time that they were open. But we have no proof of this, and stomates of some xerophytes have been known to stay open longer than in mesophytes during drought (Shields, 1950, citing others). Actually it seems very difficult to relate transpiration rate to "mesophytic" or "xerophytic" leaves (Meyer, 1927), especially when the stomate position is not considered. However, Grahle (1938) found a positive relation between transpiration and surface-volume ratios of pine leaves as well as between transpiration and amount of conducting tissue. On the other hand, numbers of stomates per surface or total leaf surface could not be related to transpiration. We also noted no relation between leaf surface and transpiration in comparing one individual plant to another, but when leaf surface was divided by root surface, a relationship to transpiration could be shown (Parker, 1949).

The smaller size of epidermal and palisade cells may be an advantage to desiccation resistance, since smaller cells are usually more desiccation-resistant (Iljin, 1935), but the highly developed palisade cells in many heliophyllous plants seem to be an adaptation to light, at least in citrus leaves (Diettert, 1937, citing Turrell), not an adaptation to drought. Pool (1923) felt that the structure of some kinds of sun leaves is such as to retard transpiration, but others have found that when well-hydrated, sun leaves transpired more than shade leaves, an idea expressed by Lamarlière in 1892 and later by Dietrich (both cited by Maximov, 1929b: 348). Huber (1925) also found this to be true in various tree species. Hanson (1917) noted that leaves on the south side of *Fraxinus pennsylvanica* and *Ulmus americana* transpired considerably more

than leaves from the center of the crown when put under the same conditions, but it would appear from Stocker's (1929b) results that "sun leaves" of *Plantago* and *Vinca* decrease much more in transpiration relative to the original rate than shade leaves when such leaves are cut from the twigs. Pisek and Winkler (1953) showed marked differences in transpirational changes during dehydration between shade and sun leaves of certain woody plants. Kramer (1949: 287) suggested that the morphological character of sun leaves could be a result of frequent loss of turgidity which checks cell enlargement and influences the total leaf area and anatomy.

A decrease in total leaf surface might be of advantage to the plant's "vital resistance", but Ashby (1932) felt that reduced external surface of *Larrea tridentata* leaves was not an advantage. Runyon, on the other hand (1934), mentioned the abscission of *Larrea* leaves during a drought and the small leaf surface per amount of twig. During a period when there was still some moisture in the soil and in the plant which was available to the leaves, this situation of partial leaf-fall could lead to better hydration of the remaining leaves and allow them to continue to metabolize to some extent instead of going into a state of dormancy. If *Larrea* leaves have a lethal level of water content at which they die or abscise, then any adaptation that helps to maintain the water content should be of importance.

b. STOMATE ACTION. The mechanism of stomate action was studied at an early time, 1856–1898, at least by von Mohl, Schwendener, G. Haberlandt and F. Darwin, and guard cell turgidity was recognized as a controlling factor in transpiration as influenced by light and leaf water content (Green, 1909: 260). According to the fundamental investigations of Loftfield (1921) and Stålfelt (1929) on herbaceous plants, stomatal movement depends largely on light when the leaf is well-hydrated, but as the leaf dehydrates, the water lack becomes progressively more effective in causing stomate closure. This idea has been confirmed for many but of course not all woody species (Stålfelt, 1932; Kramer, 1949: 287, citing several writers who worked with fruit trees and oak seedlings; Pisek and Winkler, 1953). In fact, stomate opening was believed to be a good indication of the water content of some plants (Kramer, 1949: 287, citing Maximov and

Zernova and Oppenheimer and Elze). Stocker, Rehm and Schmidt (1943) found that the more drought-resistant crop plants showed a greater ability for quick stomate closure when water content decreased, and that this therefore influenced the plant's water economy. Stålfelt (1929, 1932) found that even partial closure of stomates resulted in a decline in transpiration, and Maximov (1929: 390) stated that near-closure of stomates could be of importance to drought resistance. Evidently leaf shrinkage is concomitant with an increasing water deficit in the plant. Bachmann (1922) found that when leaves began to shrink with dehydration, the stomates had already begun to close, although he thought that the two processes were nearly simultaneous.

But there seems to be a large amount of species difference in stomate behavior. Stålfelt (1924, cited in Lundegårth, 1949: 198) showed that under the same weather conditions *Picea excelsa* displayed a different time of opening and closing its stomates than *Pinus sylvestris*. The stomates of *Coffea arabica* may close from 10 A.M. until late in the afternoon, apparently because of a light reaction and not because of reduced leaf-water content, according to Nuttman (1937). As a result, this closure was suspected to cause a reduction in photosynthesis.

Although water decline in leaves and lack of light have often been proven to cause stomate closure, other causes have been suspected. Johansen (1954) tested the effects of indole acetic acid on stomate closure but decided that in *Sinapis alba* the auxin caused a decreased water intake through the roots and that this resulted in lower leaf water content and thus closure of stomates. When leaves dehydrate, as for instance after they have been cut off the twigs, transpiration may continue for a few minutes as before, but then shows a rather sharp decline and continues at a lower rate (Huber, 1923; Oppenheimer, 1932; Walter, 1949: 248). Pisek and Winkler (1953) left little doubt that these rapid changes are caused by stomate closure; they also reported that when excised leaves which had been placed in the dark with their petioles in water were suddenly removed from the water and placed in the light, there was a momentary increase in transpiration rate, related to an opening of the stomates; then a rapid decline in transpiration as the stomates began to close with dehydration until in many woody species the remaining transpiration was almost entirely cuticular.

Other work shows the importance of stomates to water content control. Oppenheimer (1932) quoted Pearson who found that during a drought some conifers of the western United States could reduce their transpiration to low levels presumably largely because of stomate action, but Oppenheimer noted that *Pinus halepensis* leaves closed their stomates only when temperatures were "extreme" or when the air was very dry. In some evergreens of temperate regions stomate closure has been proven to be directly related to a transpirational decline (Sattoo and Hakahara, 1953). This is in line with the work of Pisek and Winkler (1953) who compared several plants for the water deficit percentage at which their stomates began and finished closing. Apparently the conifers could withstand a little more dehydration before beginning to show stomate closure (about 8 per cent of the saturation water content) than the broad-leaved species (about 3 per cent) (see also Stålfelt, 1932). Practically complete closure in both these kinds of tree leaves occurred between about 10 and 17 per cent. After this, cuticular transpiration, at least in the young leaves, was believed to be the controlling factor in maintenance of the water content; the lower the cuticular transpiration was, the longer the leaves were likely to be able to withstand drought. Ferri (1953) also found that transpiration of shrubs and trees of Brazil's "Caatinga" was greatly reduced by stomate closure in the dry season and that when conditions became more severe many species shed their leaves.

The question of the extent of stomate control over transpiration has been further considered in recent years, and in certain herbaceous species was believed to be of the greatest importance (Bange, 1953; Heath, 1954). However, it is well to recall the findings of Freeland (1948) who pointed out that in some plants gas exchange is very rapid through the unstomated surfaces and in others almost unmeasurable, so that stomate action seems to be of great importance in some plants in controlling water loss but of less importance in others.

Sometimes leaves may increase their rate of water loss towards the last stages of dehydration. This phenomenon might be explained by the fact that the stomates may open during dehydration (Iljin, 1922; Knight, 1922), but Pisek, in a special communication to the writer, stated that he doubted that this ever occurred in the leaves he worked with. According to Boon-Long

(1941), the rate of dehydration, if determined by cuticular transpiration, should decrease steadily with time. This has been demonstrated to some extent by Stålfelt (1932) and by Pisek and Berger (1938).

The fact that stomates do not entirely close during dehydration was stated by Maximov (1929b: 390) for the evergreen sclerophylls. We also concluded that stomate closure was probably not complete in *Hevea brasiliensis* leaves which had been cut from the tree. These leaves had either their upper (unstomated) or lower (stomated) surfaces coated with vaseline; the lower surfaces transpired considerably more in weak light (100 foot candles) in spite of having practically the same cuticular structure on upper and lower surfaces. When these leaves were killed by cooling to –20° C. and thawing rapidly, the stomated surfaces showed a great increase in water loss but the upper surfaces continued to transpire as before. It was also noted that in one-year-old *Abies grandis* leaves the lower (stomated) surfaces after excision transpired about half as much again as the upper (unstomated) surfaces in light of 100 foot candles and that this situation continued for several days (unpublished data). Apparently as the leaves become older, in terms of several months or years, the stomatal action is somehow weaker or the guard cell walls become stiffer, and the stomates do not close so regularly or so completely. This was indicated by Pisek and Winkler (1953) for *Picea excelsa* and independently by Parker (1954d) for *Pinus ponderosa*. We suggested that the change in transpiration with age might be accounted for by an increasing inertness of the guard cells, as mentioned by Haberlandt, possibly due to a laying down of minerals in the cell walls, as suggested by Molisch, although cuticular changes might also occur.

c. LEAF WATER CONTENT. In nearly all woody species the leaf-water content probably fluctuates diurnally in fair weather during the growing season when there is still some available water in the soil. Livingston and Brown (1912) were perhaps the first to point out that under semi-desert conditions at least a condition of incipient wilting occurred daily in leaves of certain shrubs. Marshall (1931), however, thought that Renner (1911) was probably the first to show that there are diurnal moisture fluctuations in leaves of various plants. Marshall quoted numerous

other papers from 1912 to 1922 which reported this phenomenon, and Kramer (1949: 276) cited various articles between 1933 and 1941 on the subject. Annual fluctuations in water content of evergreens also have been studied by various writers and may be of great importance to survival (discussed by Parker, 1955a).

The cause of the diurnal fluctuation in leaf-water content seems to lie, in many cases at least, in the " lag " in root-water absorption and water translocation, discussed above in the section on stems. The time of maximum decline in water content may be different in different species; for instance, Stanescu (1936) found that it reached a minimum about 2 P.M. in *Ailanthus* leaves, but about 5 P.M. in *Ampelopsis* leaves. Malin (1932), on the other hand, stated that the diurnal fluctuations in diffusion pressure deficit were about the same in conifer leaves as in many other species. Water storage cells have been described in many " xeromorphic " leaves and seem to be able to give up water to other cells and yet recover it again later under better conditions of hydration (Shields, 1950).

In other species the water content would seem to have little to do with enduring severe drought. Thoday (1921) described water contents down to 35% of the dry weight in leaves of species of *Passerina* which did not kill them. Water storage was considered to be at best of subsidiary importance to survival in these semi-desert plants. Oppenheimer (1932) pointed out the importance of the water balance to such species as *Pinus halepensis*, but he found that leaf-water content could fall to much lower levels in *Olea europaea* leaves without death occurring. The desiccation resistance in *Olea* was so striking that it seemed to him to resemble the situation in many lichens and mosses. Also in *Larrea tridentata* there is a great ability to withstand low water content, but Runyon (1934) observed that under severe drought conditions many of the leaves changed color and fell off, something that they do not do under favorable moisture conditions. This suggests that a certain lethal level of water content exists at least in the older leaves, beyond which abscission occurs. On the other hand, Duisberg (1952) felt that the amount of root has little or nothing to do with drought resistance in this species and concluded that certain chemical differences between immature, desiccation-resistant leaves and older, less resistant ones existed. But Runyon (1934)

felt that the resinous exudations which gave it the name "creosote bush" do retard water loss from the leaves. Also Runyon (1936) mentioned several other peculiarities of the more resistant leaves, including the small size of cells and, in the less resistant leaves, the larger vacuoles. He felt it was a "physiological" condition that accounted for the high resistance of the younger leaves (Runyon, 1936).

A low lethal level may also play a more important role in explaining the drought resistance of leaves of some species of oak than a high water retention (Bordeau, 1954). He found that, while the leaves of *Quercus stellata* could withstand lower moisture content than those of the less drought-resistant *Quercus borealis,* the former's leaves dried out even more rapidly than the latter's. Both species nevertheless showed a distinct lethal level and it seems clear that a certain water maintenance must be of importance. In *Artemisia tridentata* we also noted a rapid decline in water content of the leaves when they were removed from the twigs, and it was found that when the water content fell much below 50 per cent of the dry weight there was no recovery on rehydration by soaking in water as measured by the tetrazolium test (unpublished data). Nevertheless, these leaves seem capable of undergoing a wide fluctuation in water content without dying and in their natural habitat seem to be able to get sufficient water from the stems which, although having little water storage capacity, have connection to extensive and deep roots in often moist soils. Diettert (1937) felt that even a meager retention of water in *Artemisia* might be of advantage. But other adaptations are involved; one of the remarkable features in this species is the amount of venation per chlorenchyma in the leaves. It would appear that numerous adaptations are involved in this species, some of them hard to assess. In conclusion there seem to be all gradations in different plants in their water-holding capacity and in their lethal level of water content (Pisek and Berger, 1938; Pisek and Winkler, 1953), and that these two characteristics together frequently determine the main drought resistance of the plant.

d. HAIRS AND COATINGS. Various conditions of the outer surfaces of leaves have long been the subject of speculation and not so much experimentation. Hairs are often supposed to reduce transpiration without any experimental evidence to prove it. Sayre's

experiments indicated that removing the hairs from the leaf surfaces decreased transpiration instead of increasing it, possibly because the hairs themselves increase the exposed surface (Sayre, 1920, cited in Curtis and Clark, 1950: 201). This seems reasonable in view of the fact that under moist conditions, trichomes on such plants as *Crassula* can absorb water and transfer it to living cells (MacDougal, 1912, citing Marloth; Shields, 1950, citing several others). Diettert (1937), on the other hand, citing Goebeler (1886), and Wiegand (1910) would make it appear that the situation is more complicated. Diettert believed that in *Artemisia tridentata* the trichomes play an important part in lessening loss of water by transpiration, especially the glandular trichomes which secrete ethereal oils. Evidently there are in general two kinds of trichomes: living ones largely filled with cytoplasm and dead ones filled with air. According to Goebeler (1886), the presence of living trichomes on ferns greatly increases transpiration, but Wiegand (1910) found that the hairy coatings were of value on other plants in lowering transpiration when exposed to the wind, for the reason that the hairs maintained a layer of more or less saturated air over the leaf surface, an idea also expressed by other writers (cited by Shields, 1950, citing others). Yapp (1912), for instance, believed that pubescence on *Spirea ulmaria* leaves reduces transpiration. Some evidence also exists that the presence of hairs causes lower leaf temperatures (Baumert, 1907, cited by Shields, 1950), and they may have other effects of survival value.

Waxes and similar substances are often observed as an external layer on the epidermis of leaves, and various lipidic substances are sometimes laid down directly in the cell walls (for instance, Werner, 1931). But the distinction between such fatty-acid-containing materials as cutin and suberin is not entirely clear, and waxes themselves are evidently quite complex (Meara in Paech and Tracey, 1955: 380). There may also be an increased silicification of epidermal cell walls with increasing age in conifer leaves (Molisch, 1938: 103), although this would not seem to retard water loss (Parker, 1954d). Haberlandt (1928: 137) found that the corky layers of twigs of certain trees did retard transpiration to a high degree, and Kamp (1930) believed that the thickness of the cuticle of leaves influences transpiration. Waxes may be deposited on the cuticle, but Mueller, Carr and Loomis (1954) were

of the opinion that this external layer probably is not of much importance in affecting the amount of gas exchange. Their electron-microscope photographs showed how the external waxes on leaves of conifers are distributed and how they tend to wear off with increasing age. The wax on the epidermis of apples seems to increase with age, but in some kinds of apples the oil content of the cutin increases especially. This formation decreases the O_2 exchange more than CO_2 due to the behavior of these gases in passing through lipids (Hall et al., 1954).

Other exudations, e.g., the resin on *Larrea tridentata* leaves, have been suggested to be of value in retarding transpiration (Runyon, 1934), and one of his illustrations shows the resin covering the stomatal surfaces. But Duisberg (1952) pointed out that the older more drought-sensitive leaves produced more resin than the immature leaves.

In conifer leaves we have noticed the occurrence of a material, probably more resinous than waxy according to Büsgen and Münch (1929: 214) and Schwabach (1902), in the outer channels of the stomatal openings. This was observed in every age of leaf during the entire year in five species of Rocky Mountain conifer. But Haberlandt (1928: 463), drawing his information from uncited work of Link and also Wilhelm, pointed out that such plugs are granular or at least of such construction as to allow gas penetration. We have verified this opinion for *Pinus ponderosa* leaves, and have noted that the granules are worm-shaped and often separated by air spaces.

It appears that in every part of the plant there may be structures or physiological conditions that can contribute to either the overall or to the vital drought resistance. In considering all the foregoing adaptations and variations, it seems to be a great mistake to try to find a single cause of drought resistance in any one woody plant. There may be contributing factors anywhere: from the roots to the leaves, from the finest part of the cytoplasm to the most complete tissues, from the embryo to the mature plant.

Bibliography

ALBERTSON, F. W. Studies on native red cedars in west central Kansas. Kans. Acad. Sci., Trans. **43:** 85–92. 1940.

———— and WEAVER, J. E. Injury and death or recovery of trees in prairie climate. Ecol. Monog. **15:** 393–433. 1945.

ALEXANDROV, W. Sur l'intensité de la transpiration de quelques plantes herbacées. Tiflis Bot. Gard., Appl. Sect., Sci. Pap. **4**: 1–28. 1924. [Cited in Maximov, 1929b].

ASHBY, E. Transpiratory organs of *Larrea tridentata* and their ecological significance. Ecology **13**: 182–188. 1932.

BACHMANN, F. Studien über Dickenänderung von Laubblättern. Jahrb. Wiss. Bot. **61**: 372–429. 1922.

BAILEY, I. W. Contributions to plant anatomy. 1954.

BALCH, R. E. Dying of oaks in the southern Appalachians. Forest Worker **3**: 13. 1927.

BANGE, C. G. J. On the quantitative explanation of stomatal transpiration. Acta Bot. Neerl. **2**: 255–297. 1953. [Biol. Abstr. **29**: 1749. 1955].

BARTHOLOMEW, E. T. Internal decline of lemons. III. Water deficit in lemon fruits caused by excessive leaf evaporation. Amer. Jour. Bot. **13**: 102–117. 1926.

BEARD, J. S. Climax vegetation in tropical America. Ecology **25**: 127–158. 1944.

BIALE, J. B. Postharvest physiology and biochemistry of fruits. Ann. Rev. Plant Physiol. **1**: 183–206. 1950.

BIALOGLOWSKI, J. B. Effect of extent and temperature of roots on transpiration of rooted lemon cuttings. Proc. Amer. Soc. Hort. Sci. **34**: 96–102. 1936.

BIEBL, R. Vergleichende chemische Resistenzstudien an pflanzlichen Plasmen. Über "ökologische" und "konstitutionelle" Resistenzen. Protoplasma **39**: 1–13. 1949.

———. Ecological and non-environmental constitutional resistance of the protoplasm of marine algae. Jour. Mar. Biol. Assoc. United Kingdom **31**: 307–315. 1952.

BILLINGS, W. D. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecol. Monog **8**: 437–499. 1938.

BOGEN, H. J. Untersuchungen zu den "spezifischen Permeabilitätsreihen" Höflers. Planta **28**: 535. 1938.

BONNER, J. Plant biochemistry. 1950.

——— and GALSTON, A. W. Principles of plant physiology. 1952.

BOON-LONG, T. S. Transpiration as influenced by osmotic concentration and cell permeability. Amer. Jour. Bot. **28**: 333–343. 1941.

BORDEAU, P. Oak seedling ecology determining segregation of species in Piedmont oak-hickory forests. Ecol. Monog. **24**: 297–330. 1954.

BORMANN, F. H. Factors determining the role of loblolly pine and sweetgum in early old-field succession in the Piedmont of North Carolina. Ecol. Monog. **23**: 339–358. 1953.

BORRISS, H. Plasmolyseform und Streckungswachstum. Jahrb. Wiss. Bot. **86**: 784. 1938.

BOYCE, J. S. A canker of douglas fir associated with *Phomopsis lokoyae*. Jour. For. **31**: 664–672. 1933.

———. Forest pathology. 1938.

BOYKO, H., and ABRAHAM, A. Examples of root adaptability to aridity. VIII^{e} Cong. Int. Bot., Rapp. et Comm., Sect. 11 and 12: 237–241. 1954.

BRIGGS, D. R., and SIMINOVITCH, D. The chemistry of the living bark of the black locust tree in relation to frost hardiness. II. Seasonal variations in the electrophoresis patterns of the water-soluble proteins of the bark. Arch. Biochem. **23**: 18–23. 1948.

BRIGGS, L. J., and SHANTZ, H. The wilting coefficient and its indirect determination. Bot. Gaz. **53**: 20–37. 1912.

BROWN, W. V. A preliminary study of the staining of plant cells by tetrazolium chloride. Bull. Torrey Bot. Club **81**: 127–136. 1954.

BRUMBERG, E. M., and LARINOW, L. T. Ultra-violet absorption in living and dead cells. Nature **158**: 663–664. 1947.

CHU, CHIEN-REN. Der Einfluss des Wassergehaltes der Blätter der Waldbäume auf ihre Lebensfähigkeit, ihre Saugkräfte und ihre Turgor. Flora **130**: 384–437. 1936.

CLARK, J. The immediate effect of severing on the photosynthetic rate of Norway spruce branches. Plant Physiol. **29**: 489–490. 1954.

CLEMENTS, F. E. A system of nomenclature for phytogeography. Bot. Jahrb. **31**: Beiblatt 70. 1902. [Cited by Carpenter, J. R. An ecological glossary. 1938].

COILE, T. S. Soil changes associated with loblolly pine succession on abandoned agricultural land of the Piedmont Plateau. Duke Univ. School For., Bull. 5. 1940.

COOVER, C. A. Effects of drought on forest trees in southern Pennsylvania. Forest Leaves **22**: 164–165. 1930.

COPELAND, O. L. The effects of an artificially induced drought on shortleaf pine. Jour. For. **53**: 262–264. 1955.

CURTIS, O. F., and CLARK, D. G. An introduction to plant physiology. 1950.

DAUBENMIRE, R. F. Soil temperatures vs. drought as the factor in determining lower altitudinal limits of trees in the Rocky Mountains. Bot. Gaz. **105**: 1–13. 1943.

————. Plants and environment. 1947.

DE ROBERTIS, E. D. P., NOWINSKI, W. W., and SAEZ, F. A. General cytology. 2nd Ed. 1954.

DIANZANI, U. Histochemical detection with ditetrazolium chloride of some enzymatic activities in isolated mitochondria. Nature **171**: 125–126. 1953.

DIETTERT, R. A. The morphology of *Artemisia tridentata* Nutt. Lloydia **1**: 3–74. 1937.

DRAWERT, H. Zur Frage der Stoffaufnahme durch die lebende pflanzliche Zelle. IV. Der Einfluss der Wasserstoffionenkonzentration des Zellsaftes und des Aussenmediums auf die Harnstoffaufnahme. Planta **35**: 579–600. 1948.

————. Untersuchungen zur plasmolytischen Bestimmung der Wasserpermeabilität. Ein Beitrag zur Einfluss der C_H auf die Wasseraufnahme. Planta **44**: 1–8. 1954.

DUISBERG, P. C. Some relationships between xerophytism and the content of resin, nordihydroguaiaretic acid, and protein of *Larrea divaricata* Cav. Plant Physiol. **27**: 769–777. 1952.

DUNNING, D. The 1924 drought in California. Timberman **26**: 200, 202. 1925.

ECKHARDT, F. Transpiration et photosynthèse chez un xérophyte mesomorphe. Physiol. Plant. **6**: 253–261. 1953.

ELLINGER, P. Fluorescence microscopy in biology. Biol. Rev. **15**: 323–350. 1940.

Encyclopaedia Britannica. Drought. 1954.

ETZ, K. H. Über die Wirkung des Austrocknungs auf den Inhalt lebender Pflanzenzellen. Protoplasma **33**: 481–511. 1939.

FERRI, M. G. Water balance of plants from the "Caatinga". Further information on transpiration and stomatal behavior. Rev. Brasil. Biol. **13**: 237–244. 1953.

FITTING, H. Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeits. Bot. **3**: 209–275. 1911.

FREELAND, R. O. Photosynthesis in relation to stomatal frequency and distribution. Plant Physiol. **23**: 595–600. 1948.

FREY-WYSSLING, A. Submicroscopic morphology of protoplasm and its derivatives. Ed. 2. 1953.

FROTHINGHAM, E. H. Drought may result in lasting damage to stricken forest trees. U. S. Dept. Agr., Yearbook **1931**: 200–202. 1931. [Cited in Boyce, 1938].

FUNK, I. K., and WAGNALLS. New standard dictionary of the English language. 1917.

FURR, J. R., and REEVE, J. O. The range of soil-moisture percentages through which plants undergo permanent wilting in some soils from semi-arid irrigated areas. Jour. Agr. Res. **71**: 149–170. 1945.

GEURTEN. Untersuchungen über den Gaswechsel von Baumrinden. Forstwiss. Centralbl. **69**: 705. 1950.

GOEBELER, E. Die Schutzvorrichtungen am Stammscheitel der Farne. Flora **69**: 483–497. 1886.

GORDIAGIN, A. Über die winterliche Transpiration einiger Holzgewächse Ostrusslands. Beih. Bot. Zentralb. **46**: 93–118. 1930.

GRADMANN, H. Untersuchungen über die Abhängigkeit der Transpiration und des Welkens von den Wasserverhältnissen des Bodens. Jahrb. Wiss. Bot. **76**: 558–663. 1932.

GRAHLE, ANNELISE. Vergleichende Untersuchungen über strukturelle und osmotischen Eigenschaften der Nadeln verschiedener *Pinus*-Arten. Jahrb. Wiss. Bot. **78**: 203–294. 1938.

GREEN, J. R. A history of botany 1860–1900, being a continuation of Sachs' "History of Botany, 1530–1860". 1909.

GREENHAM, C. G., and COLE, D. G. Studies on the determination of dead or diseased tissues. I. Investigation on dead plant tissues. Australian Jour. Agr. Res. **1**: 103–117. 1950.

GREENHAM, C. G., NORRIS, D. O., and BROCK, R. D. Some electrical differences between healthy and virus-infected potato tubers. Nature **169**: 973–974. 1952.

GREENIDGE, K. N. H. Studies in the physiology of forest trees. I. Physiological factors affecting the movement of moisture. Amer. Jour. Bot. **41**: 807–811. 1954.

GUNZ, F. W. Reduction of tetrazolium salts by some biological agents. Nature **163**: 98. 1949.

HAAS, A. R. C., and HALMA, E. F. Relative transpiration rates in citrus leaves. Bot. Gaz. **93**: 466–473. 1932.

HABERLANDT, G. Physiological plant anatomy. 1928. [Trans. by M. Drummond].

HAIG, I. T. Factors controlling initial establishment of western white pine and associated species. Yale Univ. School For., Bull. 41. 1936.

HALES, S. Vegetable staticks. W. and J. Innys and T. Woodward. 1727. [Copy at Duke Univ.]

HALL, E. G., HUELIN, F. E., HACKNEYS, F. M. W., and BAIN, J. Gas exchange in granny Smith apples. VIII[e] Int. Cong. Bot., Sect. 11 & 12: 405. 1954.

HALL, H. M., and CLEMENTS, F. E. The phylogenetic method in taxonomy. The North American species of *Artemisia, Chrysothamnus,* and *Atriplex*. 1923.

HANSON, H. C. Leaf structure as related to environment. Amer. Jour. Bot. **4**: 533–560. 1917.

HARTIG, R. Untersuchungen an den forstbotanischen Institut zu München. II. [Cited in Büsgen and Münch. 1929: 307].

HARTLEY, C., and MERRILL, T. Storm and drouth injury to foliage of ornamental trees. Phytopath. **5**: 20–29. 1915.

HARVEY, R. B. Hardening process in plants and developments from frost injury. Jour. Agr. Res. **15**: 83–112. 1918.

HEATH, O. V. S. The part played by stomata in resistance to drought. VIII[e] Cong. Int. Bot., Sect. 11 & 12: 241–245. 1954.

HEINICKE, A. J., and CHILDERS, N. F. The influence of water deficiency in photosynthesis and transpiration of apple leaves. Amer. Soc. Hort. Sci., Proc. **33**: 155–159. 1935.

HÖFLER, K. Über Trockenhärtung des Protoplasmas. Ber. Deut. Bot. Ges. **63**: 3–10. 1950.

HÖFLER, MIGSCH, H., and ROTTENBURG, W. Über die Austrocknungsresistenz landwirtschaftlicher Kulturpflanzen. Forschungsdienst. Organ Deut. Landwirtschaftswiss. **12**: 50–61. 1941.

VON HÖHNEL. Über die Transpirationsgrössen der forstlichen Holzgewächse. Mitt. Forstl. Versuchswesen Österreichs. II. 1. 1879. [Cited by Büsgen and Münch. 1929: 302].

HOLCH, A. E. Development of roots and shoots of certain deciduous tree seedlings in different forest sites. Ecology **12**: 259–298. 1931.

HOLLE, H. Untersuchungen über Welken, Vertrocknen, und Wiederstraffwerden. Flora **108**: 73–126. 1915.

HUBER, B. Transpiration in verschiedener Baumhöhe. Zeits. f. Bot. **15**: 465–501. 1923.

————. Die Beurteilung des Wasserhaushaltes der Pflanzen. Ein Beitrag zur vergleichende Physiologie. Jahrb. Wiss. Bot. **64**(1925): 1–120. 1924.

————. Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen. Jahrb. Wiss. Bot. **67**: 877. 1928.

————. Trockenanpassungen in der Wipfel. Jour. Ecol. **19**: 283–291. 1931.

————. Die physiologische Bedeutung der Ring- und Zerstreutporigkeit. Ber. Deut. Bot. Ges. **53**: 711–719. 1935.

————. Methoden, Ergebnisse, und Probleme der neueren Baumphysiologie. Ber. Deut. Bot. Ges. **55**: (46)-(62). 1937.

————. Registrierung des CO_2-Gefälles und Berechnung des CO_2 Stromes über Pflanzengesellschaften mittels Ultrarotabsorptionsschreiber. Ber. Deut. Bot. Ges. **63**: 53–64. 1950.

————. Tree physiology. Ann. Rev. Plant Physiol. **3**: 333–346. 1952.

———— and SCHMIDT, E. Weitere thermoelektrische Untersuchungen über den Transpirationstrom der Bäume. Tharandt. Forstl. Jahrb. **87**: 369. 1936.

————. Was wissen wir vom Wasserverbrauch des Waldes? Forstwiss. Cbl. **72**: 9/10: 257–264. 1953.

HURSCH, C. R., and HAASIS, F. W. Effects of 1925 summer drought on southern Appalachian hardwoods. Ecology **12**: 380–386. 1931.

ILJIN, W. S. Über den Einfluss des Welkens der Pflanzen auf die Regulierung der Spaltoffnungen. Jahrb. Wiss. Bot. **61**: 670–697. 1922.

———— Einfluss des Welkens auf die Atmung der Pflanzen. Flora **116**: 379–403. 1923.

————. Der Einfluss der Standortsfeuchtigkeit auf den osmotischen Wert bei Pflanzen. Planta **7**: 45–58. 1929.

————. Die Ursachen der Resistenz von Pflanzenzellen gegen Austrocknen. Protoplasma **10**: 379–414. 1930.

————. Desiccation and decay of the cells of the red cabbage. Preslia XI. Věstnik Československé Botanické Společnosti v Praze. 1932.

————. Über Absterben der Pflanzengewebe durch Austrocknung und ihre Bewahrung vor dem Trockentode. Protoplasma **19**: 414–442. 1933.

————. Die Veränderung des Turgors der Pflanzenzellen als Ursache ihres Todes. Protoplasma **22**: 299–311. 1935.

IWANOFF, L. Über die Transpiration der Holzgewächse im Winter. Ber. d. deutsch. Bot. Ges. **42**: 44–49, 210–218. 1924.

JOHANSEN, S. Effect of indole-acetic acid on stomata and photosynthesis. Physiol. Plant. **7**: 531–537. 1954.

JONES, I. D., and GORTNER, R. A. Free and bound water in elastic and non-elastic gels. Jour. Phys. Chem. **36:** 387–436. 1932.
KAHL, HELENE. Über den Einfluss von Schüttelbewegungen auf Struktur und Funktion des pflanzlichen Plasmas. Planta **39:** 346–376. 1951.
KAMERLING, Z. Welche Pflanzen sollen wir "Xerophyten" nennen? Flora **106:** 433–454. 1917.
KAMP, H. Untersuchungen über Kutikularbau und kutikuläre Transpiration von Blättern. Jahrb. Wiss. Bot. **72:** 403–465. 1930.
KELLER, R., and CHIEGO, B. Vital staining of developing eggs. Protoplasma **39:** 44–54. 1949.
KESSLER, W. Über die inneren Ursachen der Kälteresistenz der Pflanzen. Planta **24:** 312–352. 1935.
———— and RUHLAND, W. Weitere Untersuchungen über die inneren Ursachen der Kälteresistenz. Planta **28:** 159–204. 1938.
KNIGHT, R. C. The interrelation of stomatal aperture, leaf water-content, and transpiration rate. Ann. Bot. **31:** 351–359. 1917.
————. Further observations on the transpiration, stomata, leaf water-content, and wilting of plants. Ann. Bot. **36:** 361–383. 1922.
KORSTIAN, C. F. Density of cell sap in relation to environmental conditions in the Wasatch Mountains of Utah. Jour. Agr. Res. **28:** 845–907. 1924.
KOSAROFF. Beih. Bot. Zentralbl. **12:** 293. 1902. [Cited in Büsgen and Münch, 1929: 308].
KOZLOWSKI, T. T. Transpiration rates of some forest tree species during the dormant season. Plant Physiol. **18:** 252–260. 1943.
————. Light and water in relation to growth and competition of Piedmont forest tree species. Ecol. Monog. **19:** 207–231. 1949.
KRAMER, P. J. Root resistance as the cause of the absorption lag. Amer. Jour. Bot. **25:** 110–113. 1938.
————. Plant and soil water relationships. 1949.
————. Effects of wilting on the subsequent intake of water by plants. Amer. Jour. Bot. **37:** 280–284. 1950.
———— and COILE, T. S. An estimate of the volume of water made available by root extension. Plant Physiol. **15:** 743–747. 1940.
KUHN, R., and JERCHEL, D. Über Invertseifen. VIII. Reduktion von Tetrazoliumsalzen durch Bakterien, garende Hefe und keimende Samen. Ber. Deut. Chem. Ges. **74:** 949–952. 1941.
KURIMOTO, T., TAKADA, H., and NAGAI, S. Physiology of *Metasequoia glyptostroboides* and related species of conifers. I. Osmotic value and salt composition of leaf saps. Jour. Inst. Polytech. Osaka City Univ. **5:** 55–65. 1954.
LACHENMEIER. Transpiration und Wasserabsorption intakter Pflanzen nach vorausgegangener Verdunkelung bei Konstanz der Lichtintensität und der übrigen Aussenfaktoren. Jahrb. Wiss. Bot. **76:** 765–827. 1932.
LAIDLAW, C. G. P., and KNIGHT, R. C. A description of a recording porometer and a note on stomatal behavior during wilting. Ann. Bot. **30:** 47–76. 1916.
LANE, R. D., and MCCOMB, A. L. Wilting and soil moisture depletion by tree seedlings and grass. Jour. For. **46:** 344–349. 1948.
LANGENER, W. Die Wasserverteilung im Stammholz der Fichte und ihre Veränderungen. Bot. Arch. **34:** 1–80. 1932.
LARCHER, W. Schnellmethode zur Unterscheidung lebender von toten Zellen mit Hilfe der Eigenfluoreszenz pflanzlicher Zellsäfte. Mikroskopie **8:** 299–302. 1953.
————. Die Kälteresistenz Mediterraner Immergrüner und ihre Beeinflussbarkeit. Planta **44:** 607–635. 1954.
LEVITT, J. Frost killing and hardiness in plants. A critical review. 1941.
————. Frost, drought, and heat resistance. Ann. Rev. Plant Physiol. **2:** 245–268. 1951.

————. The role of carbohydrates in frost resistance. VIII° Congr. Int. Bot., Sect. 11 & 12: 278–280. 1954.

LIVINGSTON, B. E., and BROWN, W. H. Relation of the daily march of transpiration to variations in the water-content of foliage leaves. Bot. Gaz. **53**: 309–330. 1912.

LOFTFIELD, J. V. G. The behavior of stomata. Carnegie Inst., Publ. 314. 1921. [Cited by Liundegårth, 1949: 201].

LOUSTALOT, A. J. Influence of soil moisture conditions on apparent photosynthesis and transpiration of pecan leaves. Jour. Agr. Res. **71**: 519–532. 1945.

LUND, E. J. Bioelectric fields and growth. 1947.

LUNDEGÅRTH, H. Klima und Boden in ihrer Wirkung auf das Pflanzenleben. 1949.

LUTZ, H. J. Occurrence of clefts in the wood of living white spruce in Alaska. Jour. For. **50**: 99–102. 1952.

LUYET, B. J., and GEHENIO, P. M. Ultra-violet absorption in living and dead cells. Biodynamica **1**(11): 1–8. 1936.

———— and ————. Effect of glycerol in limiting ice formation in tissues subjected to low temperatures. Biodynamica **7**: 107–118. 1952.

MACDOUGAL, D. T. The water balance of desert plants. Ann. Bot. **26**: 71–93. 1912.

————. Studies of tree growth by the dendrographic method. Carnegie Inst. Wash., Publ. 462. 1936. [Cited in Meyer and Anderson, 1952: 200].

MALIN, P. B. Zur Kenntnis der Saugkraft der Koniferennadeln. Protoplasma **14**: 360–460. 1932.

MARSHALL, R. Water relations of seedling conifers with special reference to wilting. Ecol. Monog. **1**: 37–97. 1931.

MAXIMOV, N. A. Experimentelle und kritische Untersuchungen über das Gefrieren und Erfrieren der Pflanzen. Jahrb. Wiss. Bot. **53**: 327–420. 1914.

————. Physiologisch-ökologische Untersuchungen über die Dürreresistenz der Xerophyten. Jahrb. Wiss. Bot. **62**: 128–143. 1923.

————. Internal factors of frost and drought resistance in plants. Protoplasma **7**: 259–291. 1929a.

————. The plant in relation to water. 1929b.

———— and KRASNOSSELSKY-MAXIMOV, T. A. Wilting of plants and its connexion with drought resistance. Jour. Ecol. **12**: 95–110. 1924.

MCINTOSH, D. C. Treatment of trees with chemicals (Stevens, Ontario). Transpiration experiment; observations of trees felled and left with foliage intact. Canada For. Serv. Mimeog. 1–141. 1949. [Cited by Smith and Goebel, 1952].

MCINTYRE, A. C., and SCHNURR, G. L. Effect of drought on oak forests. Penn. Agr. Exp. Sta., Bul. 325: 1–43. 1936. [Cited in Boyce, 1938: 52].

MEINICKE, E. P. An effect of drought in the forests of the Sierra Nevada. Phytopath. **15**: 549–553. 1925.

MEINL, G., and VON GUTTENBERG, H. Über den Einfluss von Wirkstoffen auf die Permeabilität des Protoplasmas. III. Der Einfluss des Heteroauxins auf Quellung, Viskosität, und Wasserpermeabilität von Gelatine und Agar. Planta **41**: 167–179. IV. Über die Beeinflussung des Zuckerpermeabilität von Protoplasten durch Heteroauxin. Planta **41**: 179–189. 1952.

MELLORS, R. C. Analytical cytology; methods for studying cellular form and function. 1955.

MEYER, B. S. The measurement of the rate of water-vapor loss from leaves under standard conditions. Amer. Jour. Bot. **14**: 582–591. 1927.

————. Further studies on cold resistance in evergreens with special reference to the possible role of bound water. Bot. Gaz. **94**: 297–321. 1932.

———— and ANDERSON, D. B. Plant physiology. 2nd Ed. 1952.

MILLERD, ADELE, BONNER, J., and BIALE, J. B. The climacteric rise in fruit respiration as controlled by phosphorylative coupling. Plant Physiol. **28**: 521–531. 1953.

MITTMEYER, G. Studien über die Abhängigkeit der Transpiration verschiedenen Blatttypen vom Licht und Sättigungsdefizit der Luft. Jahrb. Wiss. Bot. **74**: 364–428. 1931.

MOLISCH, H. The longevity of plants. 1938. [Trans. by E. H. Fulling].

MONTFORT, C., and HAHN, H. Atmung und Assimilation als dynamische Kennzeichen abgestufter Trockenresistenz bei höheren Pflanzen. Planta **38**: 503–515. 1950.

MUELLER, L. E., CARR, P. H., and LOOMIS, W. E. The submicroscopic structure of plant surfaces. Amer. Jour. Bot. **41**: 593–600. 1954.

NEGER, F. W., and FUCHS, J. Untersuchungen über den Nadelfall der Koniferen. Jahrb. Wiss. Bot. **55**: 608–668. 1915.

NEGISI, K., and SATTOO, T. Influence of soil moisture on photosynthesis and respiration of seedlings of Akamatu (*Pinus densiflora* Sieb. and Zucc.) and Sugi (*Cryptomeria japonica* D. Don). Jour. Jap. For. Soc. **36**: 113–118. 1954.

———— and ————. The effect of detachment on apparent photosynthesis of Akamatu (*Pinus densiflora*) and Matebasii (*Lithocarpus edulis*) seedlings. Bull. Tokyo Univ. Forests **48**: 129–138. 1955a.

———— and ————. Soil moisture in relation to apparent photosynthesis and respiration of Akamatu and Sugi seedlings. Jour. Jap. For. Soc. **37**: 99–104. 1955b.

NUTTMAN, F. J. Studies of the physiology of *Coffea arabica*. II. Stomatal movements in relation to photosynthesis under natural conditions. Ann. Bot. N.S. **1**: 681–693.

OGATA, E., and NAGAI, S. The discrimination of injury in the cells of *Porphyra tenera*. Phys. & Ecol. **6**: 10–16. 1954.

OPPENHEIMER, H. R. Zur Kenntnis der hoch-sommerlichen Wasserbilanz mediterraner Gehölzer. Ber. Deut. Bot. Ges. **50**A: 185–245. 1932.

OSTERHOUT, W. J. V. Injury, recovery, and death in relation to conductivity and permeability. 1922.

PACHTER, H. M. Magic into science; the story of Paracelsus. 1951.

PAECH, K., and TRACEY, M. V. Moderne Methoden der Pflanzenanalyze. Vol. II. 1955.

PARKER, J. Effects of the variation in the root-leaf ratio on transpiration rate. Plant Physiol. **24**: 739–743. 1949.

————. The effects of flooding on the transpiration and survival of some southeastern forest tree species. Plant Physiol. **25**: 453–460. 1950.

————. Moisture retention in leaves of conifers of the northern Rocky Mountains. Bot. Gaz. **113**: 210–216. 1951.

————. Desiccation in conifer leaves: anatomical changes and determination of the lethal level. Bot. Gaz. **114**: 189–198. 1952a.

————. Establishment of eastern red cedar by direct seeding. Jour. For. **50**: 914–917. 1952b.

————. Some applications and limitations of tetrazolium chloride. Science **118**: 77–79. 1953a.

————. Criteria of life: some methods of measuring viability. Amer. Scientist **41**: 614–618. 1953b.

————. Environment and vegetation of Tomer's Butte in the forest-grassland transition zone of North Idaho. Amer. Midl. Nat. **51**: 539–552. 1954a.

———. Physiological differences in conifer leaves of different ages. VIII[th] Cong. Int. Bot., Sect. 11 & 12: 284–285. 1954b.
———. Available water in stems of some Rocky Mountain conifers. Bot. Gaz. **115**: 380–385. 1954c.
———. Differences in survival of excised ponderosa pine leaves of different ages. Plant Physiol. **29**: 486–487. 1954d.
———. Trends in cold resistance of *Abies grandis* and *Pinus ponderosa*. Ecology **36**: 377–380. 1955a.
———. Tetrazolium salts as viability indicators: radiation-catalysed reactions. Nature **176**: 647–648. 1955b.
PERRY, G. S., and KNULL, J. N. Hemlock deaths in Pennsylvania attributed to drought. Forest worker **7**: 4. 1931.
PISEK, A., and BERGER, EDITH. Kutikuläre Transpiration und Trockenresistenz isolierter Blätter und Sprosse. Planta **28**: 124–155. 1938.
——— and SCHIESSL, R. Die Temperaturbeeinflussbarkeit der Frosthärte von Nadelhölzern und Zweigstrauchern an der alpinen Waldgrenze. [Reprinted from Ber. Naturwiss.-medizin. Vereines Innsbruck **47**: 33–52. 1939–1946].
——— and WINKLER, E. Die Schliesbewegung der Stomata bei ökologisch verschiedenen Pflanzentypen in Abhängigkeit vom Wassersätigungszustand der Blätter und vom Licht. Planta **42**: 253–278. 1953.
——— and LARCHER, W. Zusammenhang zwischen Austrocknungsresistenz und Frosthärte bei Immergrünen. Protoplasma **44**: 30–46. 1954.
POOL, R. J. Some effects of drought upon vegetation. Science 38: 822–825. 1913.
———. Xerophytism and comparative leaf anatomy in relation to transpiring power. Bot. Gaz. **76**: 221–240. 1923.
PRIESTLEY, J. H. Studies in the physiology of cambial activity. III. The seasonal activity of cambium. New Phytol. **29**: 322–354. 1930.
PRINGSHEIM, E. Wasserbewegung und Turgorregulation in welkenden Pflanzen. Jahrb. Wiss. Bot. **43**: 89–144. 1906.
RENNER, O. Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**: 171–247. 1911.
ROSENE, HILDA F. Proof of the principle of summation of cell E.M.F.'s. Plant Physiol. **10**: 209–224. 1935.
RUNYON, E. H. The organization of the creosote bush with respect to drought. Ecology **15**: 128–138. 1934.
———. Ratio of water content to dry weight in leaves of the creosote bush. Bot. Gaz. **97**: 518–553. 1936.
SATTOO, T. Relation between rate of transpiration and rate of absorption of water in seedlings of *Cryptomeria japonica* exposed to artificial wind. Bull. Tokyo Univ. Forests **37**: 19–30. 1949.
——— and HAKAHARA, N. Water relations of cuttings shortly after planting. Bull. Tokyo Univ. Forests **45**: 89–101. 1953.
——— and NAMURA, Z. Response of seedlings of *Pinus densiflora* to soil dryness. Jour. Jap. For. Soc. **35**: 71–72. 1953.
SAYRE, J. D. The relation of hairy leaf coverings to the resistance of leaves to transpiration. Ohio Jour. Sci. **20**: 55–86. 1920.
SCARTH, G. W., and LEVITT, J. The frost-hardening mechanism of plant cells. Plant Physiol. **12**: 51–78. 1937.
SCHIMPER, A. F. W. Plant geography upon a physiological basis. 1903. [Trans. by W. R. Fisher].
SCHMIDT, H. Plasmazustand und Wasserhaushalt bei *Lamium maculatum*. Protoplasma **33**: 25. 1939.
———, DIWALD, K., and STOCKER, O. Plasmatische Untersuchungen an dürreempfindlichen und dürreresistenten Sorten landwirtschaftlicher Kulturpflanzen. Planta **31**: 559–596. 1941.

SCHNEIDER, G. W., and CHILDERS, N. F. Influence of soil moisture on photosynthesis, respiration, and transpiration of apple leaves. Plant Physiol. **16**: 565–583. 1941.

SCHOPMEYER, C. S. Transpiration and physico-chemical properties of leaves as related to drought resistance in loblolly pine and shortleaf pine. Plant Physiol. **14**: 447–462. 1939.

SCHWABACH, E. Zur Entwicklung der Spaltöffnung bei Coniferen. Ber. Deut. Bot. Ges. **20**: 1–7. 1902.

SCHRANK, A. R. Relation between electrical and curvature response in the *Avena* coleoptile to mechanical stimuli. Plant Physiol. **19**: 198–211. 1944.

SCHRÖDER, D. Über den Verlauf des Welkens und die Lebenszähigkeit der Laubblätter. Diss. Göttingen. 1909.

SHANTZ, H. L. Drought resistance and soil moisture. Ecology **8**: 145–157. 1927.

SHIELDS, LORA M. Leaf xeromorphy as related to physiological and structural influences. Bot. Rev. **16**: 399–447. 1950.

————. Leaf xeromorphy in dicotyledon species from a gypsum sand deposit. Amer. Jour. Bot. **38**: 175–190. 1951.

SHIRLEY, H. L. Observations on drought injury in Minnesota. Ecology **15**: 42–48. 1934.

SHREVE, E. B. Role of sap concentration in transpiration. Carnegie Instit. Wash. Year Book **30**: 262–263. 1931.

SIMINOVITCH, D., and BRIGGS, D. R. The chemistry of the living bark of the black locust tree in relation to frost hardiness. I. Seasonal variations in protein content. Arch. Biochem. **23**: 8–17. 1948.

———— and ————. Studies on the chemistry of the living bark of the black locust in relation to its frost hardiness. III. The validity of plasmolysis and desiccation tests for determining the frost hardiness of bark tissue. Plant Physiol. **28**: 15–34. 1953.

————, WILSON, C. M., and BRIGGS, D. R. Studies etc. V. Seasonal transformations and variations in the carbohydrates: starch-sucrose interconversions. Plant Physiol. **28**: 383–400. 1953.

SIMONIS, W. Untersuchungen zum Dürreeffekt. I. Morphologische Struktur, Wassergehalt, Atmung, und Photosynthese feucht und trocken gezogener Pflanzen. Planta **40**: 313–332. 1952.

SMITH, W. R., and GOEBEL, N. B. The moisture content of green hickory. Jour. For. **50**: 616–618. 1952.

SORAUER, P. Handbuch der Pflanzenkrankheiten. Band I, Teil 1. Die nichtparasitären und Virus-Krankheiten. 1933.

STÅLFELT, M. G. Die Abhängigkeit der Spaltöffnungsreaktionen von der Wasserbilanz. Planta **8**: 287–340. 1929.

————. Der stomatäre Regulator der pflanzlichen Transpiration. Planta **17**: 22–85. 1932.

STANESCU, P. P. Daily variations in products of photosynthesis, water content, and acidity of leaves toward end of vegetative period. Amer. Jour. Bot. **23**: 374–379. 1936.

STEFANOFF, R. Studien über den Zustand und die Schwankungen des Wassergehaltes in den Blättern und Zweigen einiger Holzpflanzen. Forstwiss. Centralbl. **53**: 784–799. 1931.

STICKEL, P. W. Drought injury in hemlock-harwood stands in Connecticut. Jour. For. **31**: 573–577. 1933.

STILES, ELSA H. The drought of 1934 and its effects on trees in Kansas. Kansas Acad. Sci., Trans. **38**: 107–127. 1935.

STOCKER, O. Die Transpiration und Wasserökologie nordwest deutscher Heide und Moorpflanzen am Standort. Zeits. Bot. **15**: 1–14. 1923.

————. Das Wasserdefizit von Gefässpflanzen in verschiedenen Klimazonen. Planta **7**: 382–387. 1929a.

————. Eine Feldmethode zur Bestimmung der momentanen Transpirations- und Evaporationsgrösse. I. Eine schnellschwingende Wage als Grundlage der Methode. Ber. Deut. Bot. Ges. **47**: 126–129. II. Der Transpirations- und Evaporationsversuch. Ber. Deut. Bot. Ges. **47**: 130–136. 1929b.

————. Über die Beziehung zwischen Wasser- und Assimilationshaushalt. Ber. Deut. Bot. Ges. **55**: 370–376. 1937.

————. Beiträge zu einer Theorie der Dürreresistenz. Planta **35**: 445–466. 1948.

————. Kälte- und dürrefeste Pflanzen. [Reprinted from Die Umschau in Wissenschaft und Technik 22/20: (1–4). 1951].

————. Die Trockenresistenz der Pflanzen. VIII^{e} Congr. Int. Bot., Sect. 11 & 12: 223–232. 1954.

————. Special communication. 1955.

————, Rehm, S., and Schmidt, H. Der Wasser- und Assimilationshaushalt dürreresistenter und dürreempfindlicher Sorten landwirtschaftlicher Kulturpflanzen. II. Zuckerrüben. Jahrb. Wiss. Bot. **91**: 278–330. 1943.

Stone, E. C., Went, F. W., and Young, C. L. Water absorption from the atmosphere by plants growing in dry soil. Science **111**: 546–548. 1950.

———— and Shachori, A. Y. Absorption of artificial dew. Cal. Agr. **8**: 7, 10. 1954.

Taylor, C. A., and Furr, J. R. The effect of decreasing soil moisture supply on size of lemon fruits. Amer. Soc. Hort. Sci., Proc. **33**: 71–81. 1936.

Thoday, D. Behavior during drought of leaves of two Cape species of *Passerina* with some notes on their anatomy. Ann. Bot. **35**: 585–601. 1921.

————. The significance of reduction in the size of leaves. Jour. Ecol. **19**: 297–303. 1931.

Throneberry, G. O., and Smith, F. G. The effect of triphenyltetrazolium chloride on oat embryo respiration. Science **117**: 13. 1953.

Tiemann, H. D. Collapse in wood as shown by the microscope. Jour. For. **39**: 271–282. 1941.

Toumey, J. W. Initial root habit in American trees and its bearing on regeneration. Int. Cong. Plant Sci., Ithaca, New York, 1926, Proc. Vol. 1: 713–728. 1929. [Cited in Toumey and Korstian, 1937: 141].

———— and Korstian, C. F. Foundations of silviculture upon an ecological basis. 1937.

Tumanov, J. J. Ungenügende Wasserversorgung und das Welken der Pflanzen als Mittel zur Erhöhung ihrer Dürrreresistenz. Planta **3**: 391–480. 1927.

Ursprung, A., and Blum, G. Über die Beteilung der Kohäsion bei der Enstehung der Saugkraft in der *Pinus*-Nadel. [Reprinted from Verhandl. Naturforsch. Ges. **56**: 315–329. 1945].

Vassiljev, I. M. Über den Wasserhaushalt von Pflanzen der Sandwüste in südöstlichen Kara-Kum. Planta **14**: 225–309. 1931.

Walter, H. Die Hydratur der Pflanze und ihre physiologisch-ökologische Bedeutung. 1931.

————. Grasland, Savanne, und Busch der Arideren Teile Afrikas in ihrer ökologischen Bedingtheit. Jahrb. Wiss. Bot. **87**: 750–860. 1939.

————. Einführung in die Phytologie. Band III. Grundlagen der Pflanzenverbreitung. Teil 1: Standortslehre (Analytischökologische Geobotanik) Lieferungen 1 und 2. 1949.

Weaver, J. F., and Clements, F. E. Plant ecology. 1938.

Weaver, J. E., and Mogenson, A. Relative transpiration of conifers and broad-leaved trees in autumn and winter. Bot. Gaz. **68**: 393–424. 1919.

WEISMANN, O. Eine theoretische und experimentelle Kritik der "bound water" Theorie. Protoplasma **31**: 27–68. 1938.

WERNER, O. Die Maispflanze auf einem trockenharten Wurzelfaden vollwachsend. 1931.

WIEGAND, K. M. Some studies regarding the biology of buds and twigs in winter. Bot. Gaz. **41**: 373–424. 1906.

————. The relation of hairy and cutinized coverings to transpiration. Bot. Gaz. **49**: 430–444. 1910.

WIESNER and PACHER. Über die Transpiration entlaubter Zweige und des Stammes der Rosskastanie. Oesterr. Bot. Zeits. **5**: 9. 1875. [Cited by Wiegand, 1906].

WILCOX, J. B. KNIGHT, J. R., and BLESS, A. A. Bioelectric potentials of tumor-infected plants. Plant Physiol. **28**: 545–549. 1953.

YAPP, R. H. *Spirea ulmaria* L. and its bearing on the problem of xeromorphy in marsh plants. Ann. Bot. **26**: 815–870. 1912.

Future Contents of

THE BOTANICAL REVIEW

Articles Received and Awaiting Publication

The Ecology of River Algae	JOHN L. BLUM *Canisius College*
Fine Structure in Degraded, Ancient and Buried Wood, and Other Fossilized Plant Derivatives	J. SEN *Calcutta University*
The Plant Centrosome and the Centrosome-Blepharoplast Homology	ROBERT LEVINE *University of Rhode Island*
Chromosomal Interchanges in Plants	C. R. BURNHAM *University of Minnesota*
Fixation of Plant Chromosomes: Principles, Limitations and Recent Developments	A. K. SHARMA *Calcutta University*
Reproduction in the Bangiophycideae	KATHLEEN M. DREW *University of Manchester*
Colonization of Artificial Bare Areas by Microorganisms	WM. BRIDGE COOKE *Dept. Health, Education and Welfare* *Cincinnati, Ohio*